United States Department of Agriculture
Agricultural Research Service
Animal Husbandry Research Division
Genetics Research Council

Symposium on Inbreeding and Line Crossing as Tools in Animal Improvement

National Arboretum
Washington, D. C.
April 14-15, 1965

One of the functions of the Inter-Branch Genetics council is to sponsor educational programs designed to focus attention on research developments that are both timely and of interest on an inter-species basis. Because of the Division's current program and anticipated future research effort involving inbreeding and systems of mating, this symposium was held.

The program committee is grateful to all of the participants for making the symposium a success.

Committee Members-
R. D. Plowman-Chairman
R. E. Cook
G. M. Sidwell
H. O. Hetzer
E. J. Warwick

C O N T E N T S

Welcome Remarks and Introduction of Subject

Dr. R. E. Hodgson, Director Animal
Husbandry Research Division, ARS, USDA

It is my privilege to welcome you to this second annual meeting of the Animal Husbandry Research Division Genetics Council.

As you know, these Councils -- the Genetics Council, the Physiology Council, and the Nutrition Council -- are an inhouse mechanism through which we endeavor to bring our scientists together, scientists working in the different branches and units of the Division, for the purpose of discussing mutual problems, to review their work, to chart new courses, to get acquainted with one another, to exchange information, and, incidentally, to assist the Division in formulating proposals and programs that will advance the research program of the Division.

In this case, the Genetics Council deals with our research program on animal improvement. And as geneticists and animal breeders I would suggest that your job is ultimately to develop farm animals of superior genetic merit that are biologically efficient in the use of feed and in the physiological processes of growth, muscle development, milk production, fiber production, reproduction, and so forth.

Now, I believe that you are all quite aware of this objective and, as you pursue your work, from time to time I'm sure that you will change your tactics and approaches to the problem. But I hope that you will not change your objectives.

We are charged with the job, in concert with our counterparts and cooperators working in the different States throughout the country, to produce the kind of information that will enable our livestock and poultry producers to become more efficient in their production methods and to produce the kind of animals that will return greater profit and produce the kind of foods and fiber of animal origin that our people enjoy and desire.

Now, the purpose of this Symposium, as I understand it, is to take stock of the method of inbreeding and line crossing as a tool to genetic improvement, to find out where we stand, what we have learned and what this particular approach to the breeding program might offer for the future. In this respect it is a little bit different approach to the problem than we used last year.

I am especially pleased that we have with us to assist in going into this program several outstanding geneticists in the country that are not members of our own organization. It is excellent that these men could take time out of their busy schedules to spend these two days with us.

I also want to compliment the committee that has arranged this program. They have done a good job. I hope as each of you go back to your respective projects you will feel that your time and effort to come here have been worthwhile.

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Theoretical aspects--genetic theory and gene action involved in inbreeding and line crossing

Dr. C. Clark Cockerham, North Carolina Station, Raleigh, N.C.

I appreciate the opportunity to be here. In fact, I jumped at the opportunity.

Now, anyone in his right mind that's going to inbreed naturally cross-fertilizing organisms must have a reason. And let's start out with one possible reason. This is No. I on your handout--selection gain for individual traits of unrelated hybrids.

By "unrelated hybrids" I mean simply that no lines are used twice. Otherwise they become related and it just complicates the problem a little bit, doesn't tell us anything really different.

I have written out for you here the regular sort of projection or gain formula in terms of the response that you would get from crossing a group of unrelated lines and choosing among the hybrids on the one hand, single crosses -- threeway crosses, or double crosses. You simply plug in the conponents that are given below in one sort of prediction, or expected gain I believe it's often called.

The variance A and variance D are additive dominance and these types of variances are attributable to various kinds of gene action.

I will skip over a lot of definitions. I should think probably for a group like this that these sort of terms are something like pocket change and familiar.

Now, the assumptions are that we have a sample of lines arbitrarily inbred -- in other words, without selection -- and that the crosses reconstitute the non-inbred population. Of course, you can probably never attain this, but that will change the results only slightly.

The results indicate or illustrate the need for a high degree of inbreeding or specificity of the lines regardless of the type of cross that's being considered.

Also, while the gains are not quite proportional to the numerators, because there is a slight variation in the denominators between these various systems, they are nearly so, and so it amounts to comparing the components of variance for singles, threeways and doubles as written out in the handout material.

The relative advantage, then, of the gain, comparison of the gains, between single crosses, threeways and double crosses is a minimum of one to three-quarters to a half, you can see, if all the variance is additive. And if all the variance is dominance, the relative advantage is, of course, one to a half to a quarter.

The relative advantage of singles to threeways and threeways to doubles increases rapidly if we have much non-additive gene effects.

Now, of course, for animals, the poorer maternal performance of inbred lines may dictate the use of at least the threeway cross, and, if so, the gain on maternal performance, you see, is then in terms of the maternal single cross performance, and that of the individuals is in terms of a threeway cross.

In Item II, I have given some results to indicate the importance, let's say, of considering orders of a cross. You see for threeway crosses involving three parents you have three different ways in which the lines can be put together, and for double crosses you have four different ways.

In terms of individual traits, that is, where there are no reciprocal differences or maternal effects, the variance among threeway crosses involving the same three parent lines is given first, and second is given the variance among the double crosses involving the same four parent lines.

Now, you see in terms of threeway crosses it involves all kinds of genetic variance. And in terms of the double crosses, order would be important only if there were non-additive dominance in these types of variance.

So in terms of double crosses for individual traits, it's unlikely, I think, in general, that one would be too concerned about trying all possible ways that the double cross could be made.

But it is important, in terms of threeway crosses in terms of all kinds of variance. And in particular this is true since you are using one line as a single parent.

For maternal traits, the picture is very different, because, in terms of either the threeway or the double crosses, it would still be reflected in terms of the single cross performance, so that either in terms of threeway crosses or double crosses it would be very important to consider the order in which the lines are put together.

Rotational Crossbreeding. I don't know how popular it is any more, but I have given some results in Item III. The assumptions here are a little different, in that we are assuming to develop these relationships between a rotational cross and the type of hybrid involved, whether it's a three-line, two-line or a four-line.

It's based on a non-epistatic model -- that is, no interaction among non-allelic genes. And here we come out with the result that the rotation, the limiting mean of the rotation, is equivalent to the single cross -- and this is for the single cross -- and then there is a regression, so to speak, involving the difference between the single cross and the two parent lines, and a third of this would on the average be lost from entering into a rotational program instead of using the single cross straight out.

Now, I have not worked into these results anything concerning maternal performance.

As you see, there is less loss for the threeway and still less for the rotation of four lines.

But, on the other hand, remember that the selection gain is less. That is, the initial start is also less. And in this form it's difficult to make direct comparison.

If people are really interested, let me say we can develop this further so that some direct comparisons could be made among the various systems. It will involve, of course, inbreeding depression or the difference between hybrids on the average and the inbred lines.

In Item IV, I suppose that I'm out of line in introducing reciprocal selection into this symposium. While it is not a direct form of inbreeding, it is a procedure for developing two inbred lines with maximum hybrid performance. So in that sense it possibly does fit.

I have given the gain here for some generation of selection, for reciprocal selection, for two different initial populations, each being selected reciprocally in terms of crossbred progeny test on the other. The variances are given generally in terms of the half-sib components of variance in the crossbred progeny test.

I point out here that if you subdivide a single population, then initially a and b are just subdivisions. They are one and the same. And one can express in terms of the population variances what these half-sib components of variance are in terms of the components of genetic variance. But in time these components will be different and include dominance and other non-additive effects.

To accommodate hybrid maternal performance, of course, this procedure has to be modified to select reciprocally between two populations, say for the maternal trait, and this cross population used as a tester for a third population.

One of the reasons I included reciprocal selection was that I wanted to say a few things about it in reference to the other -- and I think in a way that maybe a lot of other people would not say it.

Now, the number and nature of the differences between hybrid and reciprocal procedures do not allow direct quantitative comparisons, or at least no one has ever done it yet. I think it could be done.

The hybrid procedure is a "pick the winner" type of selection. And the gain that we considered at first is actually for an initial test. That is, if you have a large group of lines, you make an initial test, you get an initial response, which generally is large, and at this time most of the gains -- that is, with a sufficient number of lines -- will be attained.

The hybrid procedure, of course, proceeds by recurring effort, in that new hybrids are constructed and compared with the superior ones that have already been selected.

The reciprocal procedure, on the other hand, has the inherent advantage of accumulation of genes or changes in gene frequencies, and thus the appeal of a directed process. It, as all recurrent procedures do, has the disadvantage of genetic drift and equilibria.

Equilibria are probably not important with small numbers of parents being selected, that is, with small affected population size. But, then, genetic drift is, and it is cumulative over cycles, although possible offset some by selection.

Genetic drift, on the other hand, for the hybrid procedure, is for the sum total of the program. You see, in a sense you capitalize on drift by inbreeding and making inbred lines. So that crosses then become specific, repeatable entities.

And while the distribution of genotypes in the crosses, the hybrids, may be limited in any one trial, additional comparisons in time are made which essentially broaden the genetic sampling or broaden the base and, in effect, reduce the drift for the whole program.

Well, now, with this as a backdrop, let's turn directly to the effects of inbreeding. And the reason for doing this is to consider the effect of some of the things that we might do during inbreeding and their consequences on inbreeding and on the hybrids.

Now, I have on the handout No. V just in terms of the mean, expressing it in terms of different kinds of effects considering a non-inbred population and then inbreeding it to a certain degree, where the inbreeding depression can be related to so-called dominance first-order effects, dominance second-order effects, and so on, the second order being sort of dual heterozygous effects.

There are a couple of things to note here that are important. First of all, many of the epistatic terms or interaction terms do not come into this inbreeding depression. It really involves only the all dominance types, which is reasonable in the sense that inbreeding is essentially -- what?

A reduction in heterozygosity.

The other thing is that it is linearly related to the amount of inbreeding only in terms of dominance effects. That is, first-order dominance effects.

This is because, as you see, it involves higher powers of the inbreeding coefficient in the case of two loci dominance effects, and so forth.

Now, while one cannot project the mean in such a situation, of course, some idea can be obtained by comparing or relating inbreeding depression to see if it is linearly related to the degree of inbreeding.

In terms of variance, one can say very little. If all gene action is additive, we know the whole result. The variance among lines is two times the inbreeding coefficient -- I'm talking about genetic variance, of course -- and the variance within line is one minus the inbreeding coefficient.

But I would like to stress that this is true only when all gene effects are additive. And in the general theory when we consider we have some additive and dominance variance and so forth, we can't still treat this additive part in that manner. There is a tendency to do this.

If you have partial to complete dominance, the genetic variance will increase between lines and decrease within lines -- that is, in going from non-inbred to alpha 1. But it will not be linearly related to the degree of inbreeding, and actually the variance within lines increases with inbreeding for a time for recessive genes at low frequencies.

Now, in terms of overdominance and epistasis, the results are even more variable, and about the only thing you can really say is that genetic variance disappears within lines as the inbreeding approaches 1.

You see, even for an overdominant equilibrium population with a particular gene frequency the variance will be less among homozygous lines if the equilibrium frequency is less than 0.6, and it will be greater among inbred lines if the equilibrium frequency is greater than 0.6, than in the non-inbred population.

So if you want to state what the genetic situation is, then we can always come up with: What will happen to the variances, the means and things like this?

But I am taking the approach: What can you say about some of these things without the exact knowledge of gene action, of gene frequency, and so on?

Now, the next thing I have put in is on environmental variance or stability of lines. And I did this primarily for my own fun. We actually have little theory that would lead one to speculate or say that this or that would happen with relation to stability of homozygotes, heterozygotes, and so on.

It is interesting to note, however, that if genes are additive, that is, they are additive in all environments but interact with environments, that the variance among heterozygotes will be less than among homozygotes.

And the formulae I have given here are just the value of a homozygote expressed in terms of the gene effects and environmental effect (the alphas are gene effects). And the variance below that, the variance in terms of "ii," of course, is the variance of a homozygote over environments, and "ij" is the variance of a heterozygot over environments.

It is also interesting in this respect that if the type of interaction of genes with environment is a reversal type, this will lead to average overdominance. But the basis for saying this -- and I think it is a little confusing -- is that gene action is additive in all environments, and this may be misleading in the sense that the heterozygote is intermediate between the two homozygotes.

Well, I leave that for what it's worth.

But to go beyond this, one cannot speculate again very much. Consider the case where there was a dominant gene in terms of all environments but there still was interaction with environments. Then the variance of the heterozygote would be the same as one of the homozygotes that you know. But you cannot tell or project what it would be in terms of the average of the two heterozygotes. It could be above or below.

I believe the last item on your handout is in terms of statistics of an inbreeding program. "M" is the total of parents, "N" the number of offspring, "k" the number of lines. The selection intensity within lines would be given by M as a fraction of N. The inbreeding coefficient -- depending on starting points and so forth -- is roughly as given here.

Now, "k" can vary how? That is, the number of lines. It can vary up to the number of parents divided by two, of course. And the more lines you have, the more lines that you can discard and select among lines.

The selection intensity within lines is not affected by the number of lines if the limiting factor in your facility is the number of parents that you can maintain, although it may be limited by the reproductive capacity of this species.

On the other hand, if the limiting part about your facility is "N," that is , the total number of offspring, then the number of lines is proportional to the selection intensity within lines times the number of offspring that you can maintain. And you consequently do selection then within lines at the expense of the number of lines developed.

Of course, the real situation is often in between these two.

I want to move on to consider the effect of selection within and among lines on the rate of inbreeding and hybrid performance.

Of course, as we said, the amount of selection that can be practiced within and among lines and the rate of inbreeding are interdependent.

From our first look at the response in terms of crossing, the rate of inbreeding seems to me to be of paramount importance -- or the final degree of inbreeding at least -- but I suppose not, of course, at the expense of losing all of the lines.

Now, selection within lines will improve the performance of the lines and hybrids for additive to dominant genes, and it will also increase the approach to homozygosity. This is all good. For overdominant genes, selection within lines will tend to slow down the approach to homozygosity, but the effect actually will be of small consequence in the face of fast inbreeding, such as full sibbing, and I guess should be modified except for very strongly overdominant genes which would have their equilibrium frequencies near 0.5.

Its effect on the mean of the hybrid population depends on the initial frequencies in the population. For beginning equilibrium populations, it will reduce the means of the hybrid somewhat. For epistatic genes, the results are also variable and much dependent on the exact nature of the gene effects.

As an average figure, it seems to me it is probably best to select within lines with fast inbreeding and as long as the number of lines is not appreciably reduced by doing so.

Selection, of course, will generally be effective for only a limited number of generations in terms of fast inbreeding, and it is doubtful to me that much extra effort should be expended to salvage a line in trouble but to replace it with a new one initially.

Well, so much for selection within lines. How about selection among lines?

As to the effects of selection, the conslusions are generally the same. The same ones are reached as regards gene action and selection within lines. Except here selection can have a much stronger effect.

Now, one can probably obtain as good a hybrid from the better lines as can be obtained from all lines. But, you see, the task of doing this is much greater to have both good lines and a good hybrid.

So initially it would seem best to test as many lines as possible, to gain the initial boost of selected hybrids, and then to be choosier among the lines in the further developing and testing of hybrids.

Now, how about early testing of lines in hybrid combinations?--that is, with inbreeding a quarter or a half but at some early stage?

The specificity of the hybrids and the variance among them is much dependent, of course, as we indicated earlier, on the inbreeding of the lines, particularly for non-additive effects. And as an end task the lines should have a high degree of inbreeding.

This doesn't preclude early screening of lines in hybrid performance.

Suppose, for example, you do test a group of lines in hybrid performance when the inbreeding coefficient is a half. The gain will be that as given in No. I for inbreeding of a half.

Now, if you select the lines involving the best hybrids in terms of specific hybrid combinations and now subline those and carry your inbreeding on to completion, you still have left available the extra variance indicated -- that is, that which was not accounted for in the first stage. You still have this extra variance available for later selection.

But note that the lines were not chosen on their average hybrid performance but on the basis of specific hybrids and that the parent lines of these hybrids were sub-lined and then tried in later combinations.

So I don't think this is probably the most efficient system in the sense that it takes a lot of sub-lining to make this system work. And you probably are further ahead to go on with your inbreeding program all the way.

I'll speak a little more about that later.

But right now I want to say something about the base population and the choice of a base population.

Of course, it's very, very easy to state that you would like one with the highest mean and the most variability and the greatest selection potential or limit. That's easy enough. What, in fact, you generally have are several populations, varieties, or what have you, none of which are superior in every respect.

Now, the potential gain or limit of improvement is always greatest when the populations are intermated to develop a single population as a base. This is true for the hybrid procedure or for the reciprocal procedure.

However, to be weighed against this potential gain are the initial gain and, of course, the rate of improvement, and particularly the early rate of improvement.

For the hybrid procedure, it would seem advisable to capitalize on the distinctness of inbreeding among the varieties already available and to develop inbred lines from these and cross them as an initial step.

Initial selection of populations on the basis of their cross performance, you see, works much the same as early testing and selecting lines -- that is, sub-lining. The selected populations now that you choose on the basis of their cross performance are sublined, and inbred lines develop, and then hybrid combinations are made among them.

Probably most initial gain would be made from sub-lining all the populations and test crossing them, if you had sufficient facilitie But the most expedient method and the greatest initial gain I would think would come from initially choosing the best cross populations, sub-lining these, and then choosing the best hybrids this is because by choosing the two populations that give the best cross, you have initial gain of the cross plus additional variability for selection gain.

This would hold true also for reciprocal selection. However, you have to distinguish in terms of reciprocal selection whether your goal is a large definitive program or whether it is more or less a short-term program to be possibly replaced by others in time.

But here again you get the advantage in terms of reciprocal selection of the initial gain of the cross. Such selected populations will often give a faster rate of advance in the first few generations because their gene frequencies are often different. They will not be as apt to be held back by any equilibria conditions.

However, one must admit that for the hybrid or for reciprocal selection the greatest potential, the maximum gain, is from an intermated population involving all available material.

In terms of early treatment of an intermated population base, when several are mixed or intermated, and particularly if some of them are generally undesirable, that is, some of the populations are generally undesirable, but have some special characteristics that one wants -- these are often called "exotics" in plants -- if they are included, then the resulting population, while very variable, may be quite a mess. And how should one treat such a population?

There are three alternatives that I think should come into the picture. We have considered making inbred lines for hybrids, reciprocal selection, and there's also another. One might practice family or mass selection for a while to sort of clean up the population, because such a population probably has many undesirable genes at high frequencies.

There are also questions that arise as to the number of generations of random mating that one should have before entering into either family type selection, mass selection, or entering into a program of making inbred lines or reciprocal selection.

Well, this, I will have to admit, is sort of a guess or belief on my part, but in view of the likelihood of many undesirable genes in the population, I should think that the best practice would be initially to do mass or family selection for a while.

To offset this possible advantage is that more generations of recombination may be necessitated if you are going to do this than if you are going to enter into a reciprocal program or into a program of developing inbred lines.

The number of generations of recombination is probably not too important for a large reciprocal program, in that the selection pressure will be such that over time there will be sufficient generations of recombination.

You have to worry too if you go into a fast inbreeding program whether you have allowed sufficient time for recombination so that the recombinant types can appear before inbreeding.

The last thing that I want to comment on -- no, the next to the last thing -- is combinations of reciprocal and hybrid selections.

We talked about early testing of lines and then further sublining and so forth. And we illustrated the use of hybrid populations as a means of selecting populations on which to practice reciprocal selection.

The same can be applied to the early testing and hybrid selection of partially inbred lines which, you see, could be, after an early test and selecting the combination of lines, further improved reciprocally. But I don't think this would generally be a very efficient approach.

On the other hand, after several cycles of reciprocal selection, and particularly if selection response was diminishing, then sub-lining the two populations and choosing the best hybrid might be much the most efficient and expedient way to end the process.

There are three alternatives that I think ought to go into the picture. We have considered making inbred lines for hybrids, reciprocal selection, and there is also another. One might practice family or mass selection for a while to sort of clean up a population, because such a population probably has many undesirable genes at high frequencies.

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Now, the last topic that I wanted to comment on is in terms of combinations of reciprocal and mass or family selection.

In reciprocal programs there is an inclination, of course, to want to practice mass or family selection within the population in addition to or in conjunction with the reciprocal selection. This may actually be required if one of the populations gets into reproductive difficulties. But, if so, it may well be at the expense of the reciprocal program.

Selection, as I'll stress again, within or between populations is effective for additive to dominant genes, but for types of gene action which involve the superiority of heterozygosity or balance, then intrapopulation selection will generally oppose reciprocal selection and in my opinion should be avoided.

Selection during the inbreeding procedure, on the other hand, is not as critical because of its general ineffectiveness on the one hand on the approach to homozygosity, although it may lead to a distribution of inbred lines, as I mentioned, which is somewhat less than optimal in terms of the hybrid performance.

Mr. Chairman, those are the comments that I wish to make. I think I have left a few minutes if there are any specific questions, in terms of clarification at least, I'd be happy to entertain them.

DR. KYLE: I'm not sure I understood correctly as far as crossing to determine the best populations to use either in reciprocal selection or inbreeding. Did you mean you would sub-line the separate populations, not from the cross? Which way was that?

DR. COCKERHAM: The separate populations, yes, always. Right.

In other words, the point there was that you picked the parent lines of a specific cross -- that is, you picked the package -- the cross and the lines, and you sub-line the parent lines to improve the cross, in a sense, if you want to think of it that way.

But you would not choose the parent lines on the basis of their average performance in a cross, particularly if there is non-additive gene action. I think you could lower your end result by that procedure.

DR. KINCAID: In other words, you are saying you would select the lines on the basis of how they interact with each other?

DR. COCKERHAM: And stick with those till I found something better.

DR. HETZER: Would you mind elaborating a little more on one of the last statements you made that intrapopulation selection would tend to oppose reciprocal recurrent selection if overdominance was important?

Now, the last [illegible] to comment on is in the [illegible] of [illegible] method of reciprocal and mass [illegible] family selection.

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[illegible] ill I found something

DR. COCKERHAM: Yes. It seems to me you can very easily be running yourself in circles. That was the point where you are doing selection on the one hand on cross-bred progeny tests and then you are also doing selection in the parent populations on the basis of their own performance. One could concoct many situations.

The reason for this hybrid system, of course, we think, is in terms of non-additive gene action. And if so, then these two types of selection could very well be opposing each other and just holding you on a standstill. This is the point.

DR. HETZER: Would you restrict this only to overdominance?

DR. COCKERHAM: For overdominant genes, I mean, they're easy ones.

DR. HETZER: If there are other types of genes? That's what I was wondering about.

DR. COCKERHAM: Well, for additive to dominance there's no getting around it -- Any kind of selection anywhere is fine.

FROM THE FLOOR: Would you repeat the question, please?

DR. COCKERHAM: Yes. The question had to do with this: I made some comment that I didn't think it was a good idea to practice a combination of reciprocal selection and selection within the two populations, family or other type. And the question had to do with why did I say this, I think.

DR. HETZER: To elaborate on it.

DR. COCKERHAM: Yes. I think I'm going back to that. As far as additive effects of genes are concerned and up to dominance, generally selection is all right there. The first simple case of balance, of course, is overdominance. And that involves superiority of heterozygotes. And in such cases as these, you will just be undoing on the one hand what you have been doing on the other, and vice versa. I mean it's that simple.

DR. HETZER: You are just thinking in terms of overdominance? You are not thinking in terms of other epistatic types of gene effects which would stop --

DR. COCKERHAM: Well, many epistatic models could be written where this would also hold, yes. It would involve heterozygosity on the one hand, of course, these models, superiority, or some balance, and I'm really going out on a limb in saying this a little bit, in terms involving internal balance. It still must involve heterozygosity but with a little so-called internal balance too.

DR. COCKERHAM: Yes. It seems to [illegible] it could easily be [illegible] you call it selection [illegible] the point that you are doing selection on the one hand on crosses or groups, and then you are also doing selection in the [illegible] on the basis of their own performance. You could [illegible]

[illegible] reason for this [illegible] system [illegible] in terms of non-additive [illegible] types of selection could [illegible] holding you [illegible]

DR. [illegible]: Would you restrict [illegible]

[illegible]

DR. [illegible]: If [illegible]
I [illegible]

DR. COCKERHAM: [illegible]
getting around it [illegible]

[illegible]

DR. COCKERHAM: Yes. The question had to do with [illegible] made some [illegible] that I didn't think it was [illegible] combination of reciprocal selection and selection within [illegible] family or other types. And [illegible] question [illegible] why did I say this, I think.

DR. [illegible]: To elaborate on it.

DR. COCKERHAM. Yes. I think I'm saying [illegible] as additive effects [illegible] concerned [illegible] generally selection is all right there. [illegible] of [illegible] of course, is overdominance. And [illegible] involves [illegible] of [illegible]. And in such cases as these, you [illegible] just be [illegible] on the one hand what you have been doing on the other, [illegible]. I mean it's that simple.

DR. [illegible] just thinking in terms of over [illegible]
You [illegible]

[illegible]

[illegible]

Then if these two items are put into an epistatic model, then you can have some very tightly balanced systems.

DR. KINCAID: Is the implication here that when you go after the interactions you're likely to reduce the additive part of your genetic variance?

DR. COCKERHAM: Well, this goes back to your definition. The point is in the cross, if you want to define gene effects in the cross, and variance in the cross, the thing about the reciprocal system is that it takes and puts in the additive component in the reciprocal method, what would ordinarily be dominance if you viewed it within the two populations. I don't know. Does that answer in part?

DR. KINCAID: I think so, yes.

DR. COCKERHAM: Of course, this is the whole idea it's based on.

Would you buy that interpretation, Ralph?

DR. COMSTOCK: Yes.

DR. PLOWMAN: You indicated that during the development of inbred lines it would probably be helpful and advantageous to practice selection. Now, if you do this, isn't it possible that you are selecting the heterozygote all the time and decreasing your advance in homozygosity, and if this is true, then, isn't this going to affect your subsequent crossing between lines?

DR. COCKERHAM: It will. And my comments on that had to do with first the idea that you're going to have very small lines. In this case you can't keep very many genes segregated. For very high, strongly overdominant genes with their equilibrium frequency near 0.5, you can maintain them, and selection there will oppose your approach to inbreeding.

But my reason there is I wouldn't worry about this too much. It depends on starting off with our equilibrium population and -- no, it doesn't depend on that. Because, let's see. Alan Robinson came out recently -- it depends so strongly on this middle equilibrium frequency. That is, the overdominance is so strong that its equilibrium frequency is near 0.5. It would be genes like this that you would be concerned with.

Otherwise, the problem with fixation with selection is even greater.

The trouble is that it gets tilted off. You fix a few more of the better homozygotes such that the proportions are maybe not in the best ratios for making the hybrids.

Am I making sense to you?

DR. PLOWMAN: It sounds all right.

DR. COCKERHAM: The point is selection within or between. In terms of overdominant genes, what are the best frequencies of the inbred line for all the genes? 0.5. You know. Half a line this or that. That's your best right there.

And selection depending on what you start with can help you in all ways, you see -- not all ways, but it can help you go this way or that way such that sometimes it will be beneficial, sometimes it will not.

And it seems to me that, overall, you need not be overly concerned about this particularly if you are willing to inbreed fast, to get on with the job.

Well, you're not really inbreeding with large lines.

DR. PLOWMAN: If you're inbreeding slowly, though, this would be different?

DR. COCKERHAM: Yes, this brings up some other points. I suppose they will come up in questions and discussion -- such as number of lines, rate of inbreeding. I didn't want to go on to this. To me, if you're going to inbreed, you do it the fastest possible way.

DR. PLOWMAN: Even though the product you are working with might not be productive?

DR. COCKERHAM: I believe no exceptions. If you can't do it, you can't.

DR. TEMPLE: In regard to your comment about cleaning up lines by mass selection and family selection before going into development of highly inbred lines, can you do the cleaning up job well enough by this method to keep you out of trouble later on with highly inbred lines?

DR. COCKERHAM: With enough recombination and a large enough population I believe so. Dr. Sprague can really comment on that in terms of corn experience I would think. And I don't feel strongly on this I would like to say.

DR. TEMPLE: Wouldn't it be quicker to make some matings of highly inbred nature to find out immediately?

DR. COCKERHAM: Well, the whole thing, the reason for maybe mass of family selection, was based on the assumption really -- and if this isn't so, then one shouldn't do it -- that you have a lot of undesirable genes at fairly high frequensies and for genes of this

[illegible] The [illegible] selection within or between [illegible] orchard environments [illegible] are the real differences of [illegible] are for all [illegible] U.S. [illegible] know. [illegible] this or [illegible] That's your best right there.

[illegible] comment: [illegible] which can [illegible] more [illegible] see -- not a [illegible] way, [illegible] can help you go [illegible] that [illegible] such that sometimes it will be beneficially, sometimes it will not.

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If [illegible] you're inbreeding slowly, though, this would be [illegible] not?

DR. CARKLEMAN: Yes, [illegible] brings up the other point. I suppose [illegible] question [illegible] discussion -- such as number [illegible] rate of inbreeding. I don't want to go on to this [illegible] if you're going to inbreed, you do it the fastest possible way.

DR. [illegible] though the product you [illegible] working with might not be productive.

DR. COCKERHAM: I believe no exceptions. If [illegible] you can [illegible].

DR. [illegible] in regard to your comment about [illegible] by the selection [illegible] selection before going into of [illegible] you [illegible] the planting up [illegible] will [illegible] out [illegible] later on with highly [illegible]

[illegible] combining [illegible] and a large [illegible] comment on that is [illegible] I don't feel strongly

[illegible] to make [illegible]

nature within population, the most efficient mass, family, or what-have-you selection would be the most efficient way of getting rid of them.

This is, of course, where inbreeding is with some difficulty. I mean if you have a means, like some of the plant people, where they can make umpteen, no problem, and I would give a different answer.

DR. SMITH: Well, doesn't this problem of selection both for cleaning up the defects in a mass population and also selection within lines as you inbreed really in animal populations have to do with culling out those that are more undesirable, trying to be able to advance, rather than to picking just the top select groups that you think are most desirable?

I think this might kind of counterbalance it to think in terms of culling instead of selection. It does the same thing.

DR. COCKERHAM: Fine, if you have a large enough population and can operate on a large enough base. You can't do yourself harm by mass and family selection, you see. Your heterozygote combinations remain. Those are overdominant and everything else. The problem is you don't ever do this, do you? You work with limited populations.

DR. WILSON: It seems to me that for the traits that we normally are thinking about in inbreeding and crossing I would be skeptical really that your selection within lines would have very much effect.

DR. COCKERHAM: That's right. And that's why I didn't worry about it.

DR. WILSON: I wouldn't worry about it either.

DR. COCKERHAM: I mean that's part of the reason I should think. Some people say you shouldn't select at all within lines. And the point was if you have some material, some extra offspring available in such manner that you can select, I would tend to utilize them.

DR. KINCAID: In other words, what you're saying is to inbreed as fast as you can and try to help yourself a little if you can by selection?

DR. COCKERHAM: Yes.

DR. KINCAID: It's not going to do you much good one way or the other.

DR. COCKERHAM: That's right.

[illegible]

This is [illegible] broken differently [illegible] I mean [illegible] some of them out [illegible]

DR. WILSON: [illegible] this problem [illegible] lines [illegible] you [illegible] picking [illegible]

I think [illegible] concern [illegible] terms [illegible] instead of [illegible]

DR. SCHAEFFER: Fine, [illegible] I have [illegible] enough [illegible] numerical results [illegible] overlooked [illegible] problem is you don't ever do this, do you? [illegible] population.

DR. WILSON: It seems to me that [illegible] basic [illegible] normally are thinking [illegible] inbreeding [illegible] that year [illegible] would have [illegible] much [illegible]

DR. SCHAEFFER: That's [illegible] And [illegible] about it.

DR. WILSON: I wouldn't worry about it.

DR. [illegible]: [illegible] of the [illegible] there. [illegible] simply [illegible] you shouldn't [illegible] all [illegible] lines. And [illegible] if you have any [illegible] objecting available [illegible] would tend to [illegible] that

[illegible] words, [illegible] giving [illegible] try [illegible] yourself [illegible] if you [illegible]

DR. McDOWELL: How do you derive satisfactory means for current lines when you get into your threeway crossing?

DR. COCKERHAM: For the threeway cross? What are you talking about?

DR. McDOWELL: Well, what is your "x" value in a threeway cross

DR. COCKERHAM: That's the mean of the three parent lines.

DR. McDOWELL: How do you weight this? You just take a straigh mean of the three lines?

DR. COCKERHAM: That's right. Now, in that form I don't think it's too useful and I didn't bother to go further. What you really want is Delta RS for a selected group, isn't it? And this is for a single cross. But I'll just develop the thing right here.

Now, that would, of course, depend on your gain initially from the hybrid.

Now, this selected group we can look at as the mean plus this (indicating), you see, and the parental lines of the selected hybrid can be put in terms of the mean. And I suppose the best way would say: Now, what on the average is the relationship between a parent line and a hybrid that it enters into? And we'll just call that so (writing formula).

Remember these are now the parents of the selected hybrids.

So if you do that I will come out with something like this.

$$\Delta_{RS}=\Delta_S - [\Delta_S(1-b_{XY_S}) + (\bar{Y}-\bar{X})]/3$$

Now, this in the case of reciprocal -- I could do this, you see, by substituting "T" or "D." The point is this would change from 3 or 7 or what have you.

Now, this Y minus X bar is just on the average. What is the difference between the mean of non-inbreds and your inbred lines? This would be your inbreeding depression as an average figure (indicating).

Now, I'm not so sure this is getting exactly to your question.

I often hear the statement that inbred lines are not related to their hybrids, you know. That means this (b_{XY_S}) is zero (indicating). I think on the average there probably is some relationship. That is, they are correlated a little but not to an extremely high degree.

Does this help any?

DR. McDOWELL: Just on the last point is where I have the question, and I don't know.

DR. COCKERHAM: But, you know, at least if you get into inbreeding much, you must have some idea of the inbreeding depression and how much you will lose in terms of, say, recirpocal -- I give you this too sort of tongue in check. But I think it's sort of the best projection we have available right now. I'm not sure how good it is actually. It makes a little sense.

Handout

Genetic Theory and Gene Action Involved in Inbreeding and Line Crossing

C. Clark Cockerham

April 14, 1965

I. Selection Gain for Individual Traits of Unrelated Hybrids

$$\Delta_S = \frac{k\,\sigma_S^2}{\sqrt{\dfrac{\sigma^2 - \sigma_S^2}{n} + \sigma_S^2}}$$

Δ = gain S = single crosses T = threeway crosses D = double crosses

$$\sigma_S^2 = F\sigma_A^2 + F^2\sigma_D^2 + F^2\sigma_{AA}^2 + \ldots$$

$$\sigma_T^2 = \frac{3F}{4}\sigma_A^2 + \frac{F^2}{2}\sigma_D^2 + \frac{9F^2}{16}\sigma_{AA}^2 + \ldots$$

$$\sigma_D^2 = \frac{F}{2}\sigma_A^2 + \frac{F^2}{4}\sigma_D^2 + \frac{F^2}{4}\sigma_{AA}^2 + \ldots$$

F = inbreeding coefficient of lines

k = standardized selection differential

σ^2 = total variance, genetic and environmental

n = number of crossbred individuals measured

II. Genetic Variance Among Orders of a Cross

Individual traits

$$\sigma_{OT}^2 = \frac{F}{12}\sigma_A^2 + \frac{F^2}{6}\sigma_D^2 + \frac{11F^2}{96}\sigma_{AA}^2 + \frac{F^3}{3}\sigma_{AD}^2 + \ldots$$

$$\sigma_{OD}^2 = \frac{F^2}{12}\sigma_D^2 + \frac{F^3}{24}\sigma_{AD}^2 + \ldots$$

Maternal traits (variance among single crosses from the same three lines for threeway crosses and the same four lines for double crosses)

$$\sigma_{MT}^2 = \frac{F}{3}\sigma_A^2 + \frac{2F^2}{3}\sigma_D^2 + \frac{F^2}{2}\sigma_{AA}^2 + \frac{2F^3}{3}\sigma_{AD}^2$$

$$\sigma_{MD}^2 = \frac{F}{2}\sigma_A^2 + \frac{5F^2}{6}\sigma_D^2 + \frac{F^2}{2}\sigma_{AA}^2 + \frac{5F^3}{6}\sigma_{AD}^2$$

III. Rotational Crossing

R = limiting mean of rotation Y = mean of hybrid X - mean of parent lines

$$R_S = Y_S - \frac{(Y_S - X_S}{3}$$

Limiting inbreeding coefficient for $R_S = \frac{F}{3}$

$R_T = Y_{\bar{T}} - \frac{(Y_{\bar{T}} - X_T)}{7}$ Limiting inbreeding coefficient for $R_T = \frac{F}{7}$

$Y_{\bar{T}}$ has initial response given by $\sigma^2_{\bar{T}} = \sigma^2_T - \sigma^2_{OT}$ in $\Delta_{\bar{T}}$

$R_D = Y_{\bar{D}} - \frac{(Y^*_{\bar{D}} - X_D)}{15}$ Limiting inbreeding coefficient for $R_D = \frac{F}{15}$

$Y_{\bar{D}}$ has initial gain given by $\sigma^2_{\bar{D}} = \sigma^2_D - \sigma^2_{OD}$ in $\Delta_{\bar{D}}$

$Y^*_{\bar{D}}$ varies slightly with the order of rotation

IV. Gain for Reciprocal Selection

The two initial populations are a and b

Δ_g = the gain in the gth generation

$$\Delta_g = \frac{k\ \sigma^2_{ga}}{\sqrt{\frac{\sigma^2-\sigma^2_{ga}}{n} + \sigma^2_{ga}}} + \frac{k\ \sigma^2_{gb}}{\sqrt{\frac{\sigma^2-\sigma^2_{gb}}{} + \sigma^2_{gb}}}$$

σ^2_{ga}, σ^2_{gb} are the a and b half sib components of variance in the crossbred progeny test.

In the initial generation, if a and b are the same,

$$\sigma^2_{1a} = \sigma^2_{1b} = \frac{1}{4}\sigma^2_A + \frac{1}{16}\sigma^2_{AA} + \ldots$$

but in time they will be different and include dominance and other nonadditive effects.

V. Effects of Inbreeding

a. Mean

Y_F = mean for population with inbreeding coefficient F

$Y_F = Y_0 - F\delta_1 - F^2\delta_2 - F^3\delta_3 - \ldots$

$Y_0 - Y_F = \Sigma F^i\delta$ = inbreeding depression

δ_i = ith order dominance effects summed over all loci

δ_1 = for a single locus is positive if the heterozygote is above the mean of the homozygotes

b. Variance

1. Additive only--$2F\sigma_A^2$ among lines, $(1-F)\sigma_A^2$ within lines.

2. Partial to complete dominance--Genetic variance increases among lines and decreases within lines but not linearly with F. Variance within lines increases with F for a time for recessive genes at low frequencies.

3. Overdominance and epistasis--Results are variable. Genetic variance disappears within lines as F approached 1.

4. Environmental stability--
   For additive effects only

   Homozygote $Y_{iik} = \mu + 2\alpha_i + e_k + 2(\alpha e)_{ik}$

   Heterozygote $Y_{ijk} = \mu + \alpha_i + \alpha_j + e_k + (\alpha e)_{ik} + (\alpha e)_{jk}$

   $$\sigma^2_{Yii.} = 4\sigma^2_{\alpha e} + \alpha^2_e$$

   $$\sigma^2_{Yij.} = 2\alpha^2_{\alpha e} + \sigma^2_e$$

   The results are variable with dominance and/or epistasis.

VI. Statistics of an Inbreeding Program

M = total number of parents

N = total number of offspring

k = number of lines

s = M/N, intensity of selection within lines

The inbreeding coefficient in the gth generation is roughly

$$F_g = 1 - (1 - k/2M)^g$$

$$1 \leq k \leq M/2 = sN/2$$

t/k = selection intensity among lines where k-t of the lines are lost or discarded

Experience in Plant Breeding with Emphasis on Corn.

Dr. G. F. Sprague, Crops Research Div., USDA, Beltsville, Md.

I find myself in a somewhat unusual situation. You folks are interested in inbreeding and line crosses and have done for many, many years, extensive work on mass selection, family selection, and this sort of thing.

The corn people, in reverse, for many, many years were interested in inbreeding and hybridization. The extent of use of hybrids at the present time is a good indication of the success that they have had with that procedure.

But at the present time they are becoming increasingly interested in mass selection and various types of family selection. So one or the other of us has come full circle here. I'm not sure just which.

In what I have to say this morning I'd like to divide the topic into two rather discrete portions. One I'm going to call work on population improvement, and the other aspect hybridization.

I'm going to use population improvement in a very general sense. I know that in any method of population improvement there will be a certain amount of hybridization involved, a certain amount of selection, and so on. But I'm going to use it in the general sense that anything will come under this category of population improvement that has as its objective the development of an improved variety or a pure line regardless of the methods that may have been used in the development of this sexually propagated type.

And hybridization I'm going to define as the procedure which results in a commercially utilizable F hybrid.

I think to put this in proper perspective you have to remember a little of the situation that prevailed in corn in earlier years. There grew up the general opinion that mass selection was completely ineffective. You're at a complete loss, or at least I'm at a complete loss, to account for the generality of this opinion by studying the early literature of this period, but that possibly is beside the point.

At least, the general impression was by the 1920's that mass selection as a method for improving corn varieties was completely ineffective, and for this reason, then, all efforts were devoted towards the development of inbred lines and the production of hybrids.

This general feeling persisted for many years, actually until probably the middle '40's. At this time, Dr. Hull, of the Florida Station, became very much interested in the possibility of over-dominance. The group at Raleigh became very much interested in the quantitative genetic aspects of this. And as a result of these two schools of thought, shall we say, there began to accumulate a very considerable amount of evidence in corn and in other crops as well indicating that there was a very sizable fraction of additive genetic variance.

Well, for a long period of time this accumulated evidence for additive genetic variance was more or less ignored, I think largely because no one had the courage to take this evidence at its face value and go back and see whether or not mass selection could be made to be effective.

But eventually some people at least acquired sufficient courage to go back and reexamine this whole question of population improvement through various types of selection.

I'm not going to attempt to cover this at all in any sort of historical sequence but rather in terms of population improvement methods.

Of course, the logical place to start in a review of this sort would be with mass selection.

Table 1. Mean yields for successive generations of mass selection (Gardner, Nebraska)

Population	Yield	Moisture
	Bu/acre	%
Hay's Golden (original)	79.3	17.8
1st cycle	81.9	17.8
2nd "	84.4	18.5
3rd cycle	89.8	19.0
4th "	97.4	19.2

... the ... real improvement ...
... method ... improving corn ...
... and for this reason, then, ...
... development of natural ...

... general feeling ... [illegible] ...
problem ... the middle 1940's ... at this ... Dr. Hull ... the ... Station, became very much interested in ... overdominance. ... very much ... quantitative genetic aspects of ... and ... some ... began ... very sizable amount of evidence in corn ... ing that there was a very sizable fraction of additive gene ...

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... yields for ... generations of mass selection ... (... , Nebraska)

There are two different sets of experiments on this chart. One was reported by Dr. Gardner, University of Nebraska, in 1961. And for this particular experiment he used the variety Hays Golden.

An isolated block of the variety was grown and selection practiced at harvest time, and the only major difference between the selection as he practiced it and the selection as had been practiced in earlier experiments was in a device to minimize the importance of environmental variability.

And to do this he superimposed on this isolated block an imaginary grid system at harvest time, in effect dividing the field into a series of small subplots, and then within each of these subplots selecting what appeared to be the highest yielding plants at harvest time.

A number of these were harvested, taken into the laboratory and dried, and, after drying, dry weights were determined, and the one which in fact was the highest yielding one from each subblock was then composited to form the population for the next cycle of selection.

And the results through four cycles of selection are indicated there on the chart. In effect, then, over this four cycles of selection he was able to achieve an advance of about 22 per cent in yield.

The second set of data on the right side of the table involves work done by Dr. Johnson of the Rockefeller Foundation in Costa Rica, using one of the relatively unselected Central American races but using essentially the same system of selection. At the time these data were reported, it had only been carried through three cycles of selection, and the net gain for the three cycles amounts to about 33 per cent.

So that in these two sets of data, then, the gain from mass selection in this modified form is of about the same order of magnitude as the superiority of the first hybrids which were introduced as replacements for the open pollinated varieties.

The contrast here I think needs some emphasis. This was done in three generations or four generations of mass selection as opposed to some 15 years of effort devoted to inbreeding, testing, and so on, before the first hybrids were developed -- ten to 15 years.

That is, the inbreeding programs in general were started in the 1920's. The first hybrids were released in the early 1930's.

So that you have here, for what it may be worth, a very striking contrast in yield improvement.

The next system of selection that I want to illustrate is one that we could call half-sib progeny tests, or, if we were to use the more common plant breeding term, these would be top cross tests.

Table 2. Average agronomic data recorded on the maize variety Krug and three derived second generation synthetics. (Lonnquist 1955)

Population	Acre yields	Moisture	Broken plants
	Bu.	%	%
KHII (31) 1/	87.6	13.9	13
KHII (10) 2/	87.3	12.2	16
Krug	84.7	13.1	10
KLII 3/	69.4	11.1	5

1/ High yield selection involving 31 lines in the first cycle.

2/ High yield selection involving 10 lines

3/ Low yield selection.

Individual selected plants would be crossed to a common tester variety. These test crosses then would be evaluated in yield trials. The highest yielding combinations would then be recombined on the basis of remnant seed of the tested parents.

This represents a series of such comparisons which was made at the University of Nebraska. The parent variety here was Krug. That is what the "K" stands for. The "H" and "L" stand for high and low yield selections. The Roman numeral II indicates that it's the second cycle of such selection. The figures in parentheses are the number of lines that were recombined to form this new varietal synthetic.

The tester parent here was the parent variety, so that this represents then attempts to make an improvement within an existing open pollinated variety.

The yield of the Krug parent variety in this material was 84.7 bushels per acre, and you'll notice that the two highest selections are somewhat higher than this with no difference between the 10-line composite and the 31-line composite.

Those yield increases over the parent variety are significant only at the 10 per cent level.

Selection for low yield was much more effective. There is a decrease there of some 15 bushels. That, of course, is highly significant.

So the indication here is that this half-sib progeny selection has been somewhat effective, not as effective as the mass selection material we saw earlier, but I think any attempts to make critical comparisons between these different selection systems may be misleading because of the fact that they involve different parental varieties, different sets of operational systems, and so on and so forth.

The next system of selection that we might give some attention to is somewhat comparable at least, to the half-sib selection system that we were just looking at, although this is not entirely true. This would involve the fairly extensive ear-row trials, ear-row breeding methods that were used for yield, for oil and protein, and so on.

The use of the term "half sib" here is not quite correct, because these are really a combination of half sibs, full sibs, and every other kind of sibs that you can think of with no possibility of disentangling the relationships.

And here we have a rather peculiar situation in some respects. I think you're all familiar with the classical Illinois experiments on selection for high and low oil and high and low protein. These are somewhat unique as far as experiments go because they have now been in existence something over 60 generations. There is no indication of any appreciable plateauing at all as far as increases in oil percentage or protein percentage are concerned.

There is some possible suggestion of a plateauing in the selection for low oil. This is undoubtedly genetic. But it has I think a somewhat peculiar genetic basis, because in the low oil stocks there has been a very pronounced accumulation of genes which condition germless and miniature germ. And, of course, the bulk of the oil in the corn kernel is in the germ. So you don't make much progress for selecting for low oil if the parental selected ears are germless. You don't get much progeny from things of this sort.

So that we have the classical experiments on high and low oil which indicate a very marked degree of progress. Corresponding to this are selections for yield which were conducted for a much shorter period of time. But in these the results are quite different.

Again, comparable to the data that you just saw, selection for low yield was quite effective. Selection for high yield was of rather dubious significance.

So much for that type of selection.

We'll go on, then, to the next table, which involves a system of full-sib family selection.

Table 3. Yield in pounds per plant for full-sib family selection in each of 4 populations.

Population	Cycle of selection					Gain per cycle in percent of mean	
	0	1	2	3	4	Observed	Predicted
Jarvis	.396	.369	.460	.469	---	6.1	6.7
Indian Chief	.399	---	.458	---	---	7.4	5.5
$(NC7xCI.21)F_2$	.362	---	.386	.400	.398	2.5	9.3
$(NC34xNC45)F_2$	.267	---	---	.279	---	1.5	11.5

These are results from the North Carolina Station. These were reported in the Maize Genetics Co-op Newsletter of two or three years ago and have not appeared as yet in print.

But they compared the two open pollinated varieties Jarvis and Indian Chief which have been used very extensively in the North Carolina program. And you can see that there is a rather close agreement between the observed and predicted gain per cycle in per cent of the mean.

In comparison with these two open pollinated varieties, comparable full-sib family selection was practiced in two different F_2 populations, involving crosses between highly inbred parental lines. And there is a decided contrast in these two as compared with the varieties.

The predicted gain is somewhat higher than with the open pollinated varieties, and the realized gain considerably lower.

I'm not entirely sure just what this means, but we'll see this same thing recurring in some of the other data that we will look at a little later on.

One of the other systems of selection would involve the development of S_1 lines, the evaluation of these S_1 lines by some criteria or other depending upon what the character of interest was, recombining these S_1 lines into a new synthetic population, and then repeating the same cycle of inbreeding, recombination, and so on.

The amount of data bearing on this is rather limited.

Table 4. Mean oil percentages for a recurrent and selfing series

Series	Mean oil percentage for the period indicated					Total gain	Gain per generation
	S_1	S_2	S_3	S_4	S_5		
Selfing	5.0	4.6	5.0	5.2	5.6	0.6	0.12
Recurrent population	4.2		5.2		7.0	2.0	0.40
Selected sample	5.0		7.2		8.2	3.2	0.64

This is one set of data which involves oil percentage of the kernel. And in this series it started with the same base population. A sizable number of ears were individually analyzed for oil percentage, and ten of those with the highest oil percentage saved for inclusion in this particular experiment.

Duplicate seed lots were taken from these ten ears, and in one series the material was carried on by continuous inbreeding, selecting in each inbred generation those ears which had the highest oil percentage. Then in the other series the ten parental lines were intercrossed, and then from this synthetic population a new cycle of selfs were obtained, and so on.

So the size of the population to the number of oil analyses, the number of pollinations required, and so on, were essentially similar in the two series.

You will notice that in the selfing series over the five generations involved that there was a total gain of six-tenths of a per cent of oil, or, stating this in terms of gain per generation, about .12 of a per cent of oil.

In the recurrent series, or the one recombining selected S_1's, we have two comparisons listed there, one which we have called the recurrent population. The figures given there are for the mean of all of the ears analyzed.

And here you can see that there was a considerable increase in net gain.

Or we can take the lower set of figures, which involve only the selected parents in each generation or in each cycle. It doesn't make too much difference which of these two sets of figures you use. The gain is materially greater per generation than under the selection, selfing and selection.

There were rather striking differences in the gains made within-- Or there were striking differences between the ten lines involved in this composite and the figures that are the average for the whole group.

Now may we have the next slide, please?

So far we have been talking entirely about corn and possibly I should have had this next table in at an earlier point. But the opportunities for selection in a self-fertilizing crop are, of course, somewhat greater than we usually think would be true for random mating populations.

On the other hand, in many of these self-fertilizing crops it is possible by means of genetic tricks of one sort or another to make them, in effect, random mating populations. And this is what is involved in this present set of data.

Table 5. Winter survival in successive cycles of a male sterile composite cross of barley 1/

	Year of test 1958 2/	1963 3/
Ms comp. cross (bulk parents)	100	100
1st cycle	84	
2nd "	113	
3rd "	125	
4th "	126	145
5th "		162
6th "		156

1/ These data were supplied by Dr. D. A. Reid, and are taken from the Barley Winterhardiners Nursery Report.

2/ 25 locations.

3/ 17 locations.

This involves natural selection for winterhardiness in barley. And the way they approached this was to take a series of their most winterhardy varieties. These were individually crossed to a genetic male sterile type. These were back crossed then to the variety for a number of generations to minimize the genetic contribution of the male sterile type, retaining, of course, the male sterility in the course of this back crossing, and then these populations were combined, these varieties were combined.

I won't go into all of the details of the experiment. It's enough I think for our present purpose to say that after the population was once established, seed was saved only from the male sterile plants. This, in effect, then, gives you a random mating population.

And the results here indicate the progress that has been made in winterhardiness under this particular regime.

The male sterile composite cross is given the value of 100, and then comparisons were made. Two sets of comparisons were made, one in 1958 using remnant seed that had accumulated and the second comparison in 1963.

Unfortunately, the two are not directly comparable because of difficulties with quantities of remnant seed.

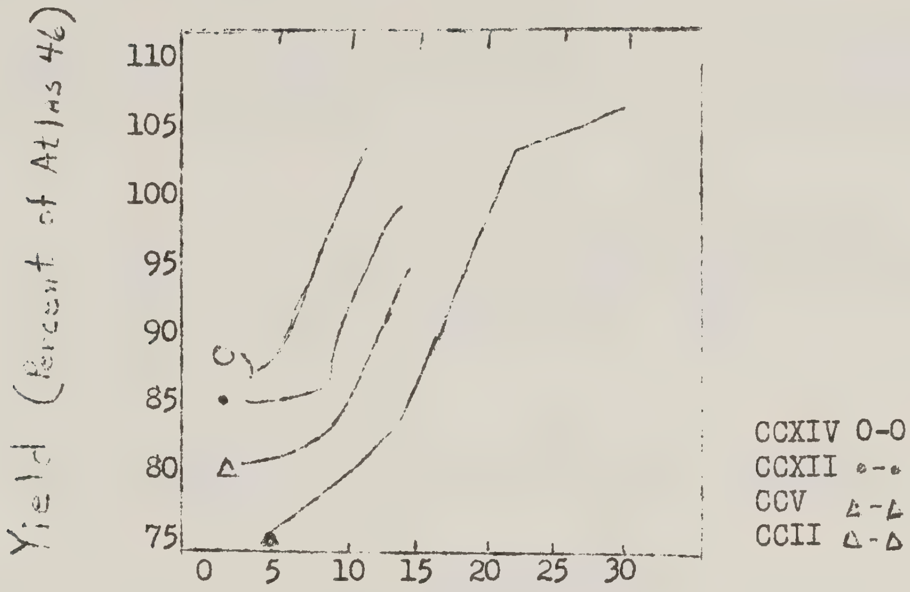
But whether you take the 1958 data, which involves four cycles of selection, or the 1963 data, which involves three additional cycles of selection, there is evidence here for a very considerable amount of progress.

Now, here it's somewhat more difficult to interpret this progress than it would be in the ordinary selection experiment, because you have no control over the selection intensity. You are entirely dependent upon the severity of a particular winter as to how many of the plants in the population are killed, so that it's not subject to as precise analysis as you might wish.

But I think it's quite apparent that a considerable amount of genetic gain has been achieved.

In the next table I would like to call your attention only to two of the lines shown on this graph, the bottom one and the top one.

Figure 6.



The bottom line represents an intercross population. It has used a large number of varieties of barley. These, of course, would be comparable to inbred lines, highly inbred lines.

These were crossed in all possible combinations and then the hybrid seed bulked and propagated under mass conditions allowing for natural selection.

Now, the amount of crossing, natural crossing, in barley is rather low, so that essentially this is just mass selection in a highly heterozygous and heterogeneous population.

You will notice over the 30 generations in which this population has been maintained there has been a very, very material increase in yield.

Actually, from this population there have been a rather large number of varieties selected which are now in extensive commercial use in the western part of the United States.

The top line represents a population which was established at a much later date in time but again making use of this genetic device to establish a random mating population through the incorporation of a simple genetic factor for male sterility.

And, of course, it starts at a much higher point on the graph, because there were a larger number of high-yielding varieties available at that time.

It has not progressed far enough to draw any very general conclusions. But the suggestion is that it may have a somewhat different slope than the base line, and certainly the opportunities for improvement there for total realized gain seem to be very, very good.

The results as far as they are available from the self-pollinating crops seem to parallel those from the random mating populations if devices can be used to in fact make them random mating populations or at least something comparable to random mating populations.

Well, that represents the series of illustrations that I wanted to use which have a bearing on population improvement.

We will then go on to various sorts of experiments which to some extent have a bearing on population improvement but more particularly I think are concerned with hybridization.

Terminology has grown up in the plant group of general and specific combining ability. I have some responsibility for this, and I think every time this came up for discussion with Professor Kempthorne at Ames he always carefully explained to me how much better it would have been had these terms never been used.

But, nevertheless, they have been used. And some of the recurrent selection schemes that I am going to talk about were devised back in the days when we thought some of these systems had possibly more significance than we would be willing to accord them at the present time.

The first one is what we called recurrent selection for general combining ability. General combining ability, of course, involves primarily additive genetic effects. And the tester parent in this particular case was a high-yielding double cross population, or high-yielding double cross but one which was quite susceptible to lodging.

Table 7. Yield data from a recurrent selection scheme involving Stiff Stalk Synthetic and Iowa 13 as the tester parent (Penny et al. 1963)

Generation	Test cross yield trials: Ia 13 Bu/A	Test crosses Bu/A	Calc. 1/ genetic advance	1958-59 yield trials: Selected population X Ia. 13	Observed genetic advance
C_0	88.9	82.3	10.1	104.8	----
C_1	86.1	85.9	5.9	102.3	1.4
C_2	104.3	104.2	6.5	108.0	5.6
C_3	74.3	72.1	0.0	108.0	0.0
C_4	103.6	111.3	3.1	110.0	1.9

1/ Genetic advance = $(\bar{x}-x)\ s_g^2\ 1(s^2g + \frac{s^2gt}{t} + \frac{s^2}{rt})$

At the time this particular series was started, we felt that one of the major difficulties with the hybrids that were then being grown was that they didn't possess enough resistance to root and stalk lodging, and so we were interested in attempting to develop new populations or new hybrids which would be improved in this particular respect. That's why we chose this Lodging-susceptible tester parent.

The general procedure here would be to self individual plants in the Stiff Stalk Synthetic, which, in turn, I possibly should explain, was a synthetic made up by intercrossing 16 inbred lines.

This synthetic then had been maintained for a number of generations by random mating under isolated conditions so that presumably it had made some approach at least to equilibrium conditions.

Individual plants in this Stiff Stalk Synthetic were self-pollinated and outcrossed to the tester parent. Yield trials were then conducted of these test crosses, and on the basis of test cross performance the highest yielding combinations were recombined through the remnant seed of the self-pollinated parent.

The data represented here are for four cycles of such selection and you will note that the progress achieved has been slight.

The next set of data are a companion series to a table presented earlier involving population improvement, through use of half-sib progeny tests. There we were considering the performance of the recombined selected material as a population. Here we are considering it from the standpoint of its hybrid combining ability or what it does in hybrid combinations.

Table 8. Yields and genetic variance estimates obtained with test-crosses of Krug lines under different breeding systems (McGill and Lonnquist 1955)

Source of test-crosses	Number of crosses	Mean yield bu/A	g^2_p 1/
$KH_{11}(31)$	76	97.5	0.392
$KH_{11}(10)$	75	97.9	0.374
"High" lines	22	97.1	-----
Krug (original)	76	92.4	0.815
KL_{11}	75	90.1	0.245
"Low" lines	8	90.5	-----

1/ Estimated genetic variance among test crosses.

The selection for low yield you remember from the standpoint of the recombined population was effective. These low-yielding synthetic and the lines derived from this low-yielding synthetic are lower in yield than the parental variety.

The ones which were selected for high yield are higher than the parental variety, indicating that the selection that was practiced at the population improvement level has carried over to the performance of this same material in hybrid combinations.

Now, I refer you to the next table.

Table 9. Average yields and observed and calculated genetic advance for successive cycles of recurrent selection for specific combining ability (Penny et al. 1963)

Cross	Yield Bu/A	Genetic advance % Calc.	Genetic advance % Obs.
Lancaster C_0xHy	76.4	----	----
" C_1xHy	80.3	3.4	5.1
" C_2xHy	82.9	18.6	8.1
Kolkmuin C_0xHy	69.1	---	---
" C_1xHy	76.1	5.1	10.1
" C_2xHy	89.1	11.8	26.3
Alph C_0xB14	113.3	---	---
" C_1xB14	117.4	16.7	5.5
" C_2xB14	127.3	8.5	8.4
(WF9xB7)C_0xB14	119.8	---	---
" C_1xB14	123.4	7.1	3.0
" C_2xB14	123.6	7.2	0.2

If you remember the background I gave you before, this would be another instance of recurrent selection for general combining ability. It has gone through four cycles of selection, and you'll notice that there has been some gradual improvement, not too regular but at least some indication of a trend.

The general indication here I think is that we have made progress at the rate of something a little over one bushel in yield per cycle, which is not a very dramatic increase for the amount of labor involved in an operation of this sort.

Then this illustration involves what we have called recurrent selection for specific combining ability. And here I think we have to be a little careful. This differs in procedure from recurrent selection for general combining ability only in the choice of the tester parent used.

In the case of recurrent selection for general combining ability we have used a heterozygous and heterogeneous tester--in other words, giving as great emphasis as possible to additive gene effects. And in the case of recurrent selection for specific combining ability we have used a highly inbred parent as the tester.

This, in theory at least, might be expected to give greater emphasis to overdominance effects, epistatic effects, and things of this sort.

But you have to remember that this distinction may, in fact, be rather meaningless. Merely because you say you are running an experiment on recurrent selection for specific combining ability doesn't necessarily imply that the only types of gene action that you are going to measure will be those involving overdominance or epistatic effects.

Well, there are data here for two different sets of experiments. The first one involves two different open pollinated varieties, the varieties Lancaster and Kolkmeier. And the common inbred parent was the line "Hy," a line which is in very extensive commercial use. You will notice that there has been a considerable genetic gain realized.

The agreement between the calculated genetic gain and the observed genetic gain is not always as close as you might wish, but in both the Lancaster series and in the Kolkmeier series there have been fairly substantial increases in yield as a result of this selection.

We have a somewhat comparable series in the lower half of the table. The variety Alph was a very long-eared type that we picked up in southern Iowa a good many years ago, and paired with that we have used a single cross combination, WF9 x B7, which was one we were very much interested in at the time these particular experiments were initiated.

The comparison again is similar to that in the upper half of the table, that there has been significant increase in yield at least in the Alph series, a somewhat disappointing increase in the yield in the WF9 x B7 series.

I would like to point out here that we saw in the full sib family selection data from North Carolina that the realized gain from full sib family selection in F2 populations derived from crossing highly inbred lines was rather low, we have the same situation here with respect to recurrent selection for specific combining abilities.

Now, there is one other point that I'd like to make on this. This particular experiment was set up to try and give us some information on the possible importance of overdominance.

And our general reasoning was of this sort: That if the realized gains in a selection program of this sort were due primarily to dominance or additive effects that there should be a gradual shift in the gene frequencies of the population, and whatever improvement was made in the population should be represented in hybrid combinations between the two halves of the experiment, for example, between Lancaster and Kolkmeier.

On the other hand, if the gene action involved was primarily due to overdominance, then the effective selection would again change the gene frequency of the population but would change it in such a way that it would be the exact complement, at the limit -- would be the exact complement of the gene frequency of the tester parent.

And since these two populations were undergoing the same sort of selection, then, when the Lancaster and the Kolkmeier were intercrossed, we would expect a decreasing yield trend. In the case of additive or dominance effects, we would expect an increasing yield trend.

The results that were obtained in this particular set of data --and there have been other sets since -- indicate that all of the improvement which has been realized in performance relative to the inbred tester parent has been retained in the crosses between the different cycles.

In other words, the cross of Lancaster C_1 by Kolkmeier C_1 reflects the same general level of improvement as indicated by Lancaster C_1 by Hy or Kolkmeier C_1 by Hy.

So that although, according to the designation that is given to this particular system of recurrent selection, we would expect that we were selecting for nonadditive effects, in actual practice it turns out that the gains we have achieved, have been due apparently almost entirely to additive effects.

Now the final set of data.

Table 10. Average yields and observed and calculated genetic advance for successive cycles of reciprocal recurrent selection.

Cross	Yield	Genetic advance	
	Bu/acre	Calc.	Obs.
$SSSC_0$ x $CBSC_0$	76.3	---	---
$SSSC_1$ x $CBSC_1$	81.1	2.3	4.8
$SSSC_2$ x $CBSC_2$	84.1	9.8	7.8
Mean D. C. checks	84.9		

This involves reciprocal recurrent selection in which we use two different synthetics. One was the same Stiff Stalk Synthetic that we referred to earlier. The second one is one we have called Corn Borer Synthetic.

This again is a 16-line synthetic in which the parent inbreds that were used represented as of that date the most highly resistant group of lines that we had to the European corn borer.

At that time we were quite concerned about the losses that were being realized from the European corn borer, and we felt that we might be able to achieve two objectives from this experiment, one to get some general information on the relative effectiveness of reciprocal recurrent selection and at the same time improve the level of corn borer resistance of the population.

You can see that there has been a fair increase in yield as a result of this selection scheme. It amounts to about two and a half bushels I believe per cycle or about eight-tenths of a bushel per year.

Now, again, at the time that this particular experiment was set up, our general feeling was that these two populations should be kept distinct, that we would have an advantage by doing this. I think the general feeling at the present time is that we would have been better advised had we intercrossed these two populations, allowed them to intermate for possibly a short period of time, and then in some way or other divided them into two separate sub-populations.

I think that this in general would be true unless overdominance was, in fact, a very important type of gene action. I don't want to go into that in detail, but there is very little critical evidence available at the present time in corn indicating that overdominance is of any great importance.

I'll be glad to try and answer any questions, but that's all I have to present.

DR. HETZER: I'd like to ask you a question. In one experiment you were selecting for general combining ability and in another one you were selecting for specific combining ability. And if I interpret your slides correctly, you made more or greater progress in selecting for specific combining ability than for general. Yet you didn't seem to think it was mostly additive types of gene effects that were involved in both.

I was wondering if you had any explanation for the difference in the rate of greater progress or the total progress made by these two schemes.

DR. SPRAGUE: Well, we, of course, like to compare these different schemes in terms of rate of progress, but I think this is a very, very hazardous procedure, because you are starting with populations which are quite different. The experiments were run under different sets of environmental conditions involving different years, different locations, and things of this sort, so that I think it's quite hazardous at the moment to make any direct comparisons between any of these selection schemes.

There have been some data reported from the Florida Experiment Station comparing the use of a broadbase tester parent which would measure, in the same line of argument we used earlier, additive effects primarily, and also using an inbred line as a tester parent which would be comparable to what we were calling recurrent selection for specific combining ability.

Their data probably bear a little more directly on this than the data which I just covered. But their results again would indicate that they had made more progress using the inbred line as a tester parent than in using a broad-base heterozygous and heterogeneous tester parent.

DR. WARWICK: Dr. Sprague, there have been several years of evidence accumulated now on some of these recurrent selection procedures. Where do you stand in corn breeding today so far as using this technique to improve hybrids? In other words what is the comparison between the yields from some of these and some of the hybrids developed by the more conventional inbreeding and hybridization techniques?

DR. SPRAGUE: Well, in both the recurrent selection for specific combining ability series of material and the reciprocal recurrent selection material at Ames at the present time, the selected sample times whatever the tester parent is--the hybrid produced in that way--would compare relatively favorably with the standard commercial hybrids. So that I think is a partial answer to your question.

There is a growing feeling I believe among most of the corn people that they have inbreeding and hybridization programs under way with a large number of lines that are in various stages of development, and they, of course, are not going to give up this investment at the present time.

I think, on the other hand, there is a feeling that in the long-range developments looking forward to the development of new hybrids sometime hence that their best approach would be to first make whatever gains were possible by some form of selection, whether it's mass selection, full sib family selection, S_1 progeny selection, any of these selection types, and to make as much gain as possible from the additive gene effects, and then only after this gain had been realized would they go to some of the recurrent selection approaches, probably reciprocal recurrent selection, for their final improvement of the material.

There is quite a little of this actually being done. Many of the seed companies have experiments of this sort under way in the development of new populations which they would hope eventually to either introduce into reciprocal recurrent selection programs or go back to the conventional inbreeding and hybridization approach.

DR. KING: Dr. Sprague, most of the slides just show the different cycles of yield without any indication of whether any procedures are used to adjust for year effects.

DR. SPRAGUE: I should have mentioned all the data I showed on the slides were directly comparable. We can do this relatively easily in corn by use of remnant seed. All of the data that were shown there were directly comparable.

In other words, all of the material would have been compared in the same series of yield trials. In some cases they represented the average of two or three years at two or three locations. They were all directly comparable.

Inbreeding and Linecrossing Experience In Laboratory (and other) Species

W. H. Kyle

For purposes of efficient improvement of classes of livestock which do not produce litters, the use of an inbreeding and line-crossing system is strictly "for the birds." This extreme point of view, possibly shared by some of you, has been reached after experience with a variety of species. In fact, inbreeding and line-crossing may be only slightly advantageous for the birds (egg type), but the poultry experts will present their decision later.

Few of us would question the need for a high level of hetero-zygosity in traits of reproduction in nearly every animal species. However, we sometimes forget that selected strain-crosses can also provide a high level of heterozygosity. We have often been excited by an expression of heterosis in line-crosses without realizing that we were merely getting back what we had spent years in losing through a difficult program of inbreeding.

As you all know, selection is still the keystone of animal breeding, and yet so many facets of this force remain untouched. It is interesting to speculate on how much farther advanced livestock breeding would be today if the great pre-occupation with inbreeding twenty-five years ago had been replaced by a major attack on experi-mental selection techniques in a wide variety of stocks.

With respect to inbreeding, it is well-known that major gains cannot be expected unless intense selection is practiced among lines on the basis of crossing results. Because of the small numbers of lines and the difficulty of crossing, the situation in large animals is rather hopeless unless blind luck attends the animal breeder's efforts. Further discouragement awaits the large animal breeder who has found the pearl in the oyster. He needs two matched pearls for effective improvement, and they are rare indeed. Because average female replacement time is four or five years, he must be content to pursue a program of rotational top-crossing with his valuable inbred lines. Should we accept this kind of odds for large animal improvement?

To descend from sublime generalities to a ridiculous little insect, let us look at some results in Tribolium castaneum, a flour beetle. The measured trait was 14-day larval weight. Each of the ten treatment groups in each replication was initiated with identical pedigrees from 44 full-sib families. The treatments were mass selection (M) and random selection (R) in combination with each of the five mating systems: inbreeding (i), outbreeding (o), assorta-tive (a), disassortative (d) and random (r). In each subclass in each of the two replications, 120 offspring were individually weighed each generation from a maximum of 20 of the 22 single-pair matings. The experiment was carried through eight generations of selection. Most of the work was a thesis project of Paul Blair at Purdue.

Heritability of larval weight was estimated to be .15 ± .03 in the foundation generation, and heterosis in original single crosses to form the population was 34%.

The increased cost of inbreeding appeared quickly. Because of higher sterility, it became necessary in the second generation to increase the number of matings from 22 to 26 in only the inbred subclasses. Average sterility of the two replications from generations 2 through 8 was 27%, 30%, 13% and 12% for Mi, Ri, Mr and Rr, respectively.

The average inbreeding coefficients over both replications in generation 8 for Mi, Mr, Md, Ma and Mo were .24, .06, .04, .03 and .01, respectively, The similar coefficients for Ri, Ra, Rr, Rd and Ro were .19, .05, .02, .02 and .00, respectively. Selection was practiced with no adjustment for inbreeding.

The inbred subclasses had significantly larger phenotypic variances than any other mating system, but realized heritability for the inbreds was lowest of the selected (M)groups.

A terminal test (t) with controls was carried out in which the two replications of certain subclasses in generation 8 were crossed. as before, 120 offspring were weighed in each subclass. Also at this time, a cross of two full-sib lines (F_{st}) was made. When the subclasses were established in generation zero, twenty full-sib single-pair matings were made from the families for each replication. After the first mating, each line was maintained by mating five sib pairs in each generation, if possible.

After 9 generations, only 4 lines remained and only two of these had enough progeny to line-cross. The following list shows the terminal test results and the averages of the two replications for certain subclasses in generation 8:

Mean 14-day larval weight (micrograms) in generation 8
and the terminal test

M_o	2920	M_i	2412
M_{ot}	2878	R_{it}	2250
M_a	2789	R_{rt}	2250
M_r	2742	R_r	2115
M_{it}	2729	F_{st}	2072
M_d	2711	R_i	1885

The groupings are nearly accurate. Clearly all mass-selected subclasses are superior to all random-selected subclasses, whether or not the latter are crossed. Outbreeding is superior and crossing its

replicates depressed merit slightly. Inbreeding (M_i)is the poorest mating system for selection. It is significantly lower in merit than all other selected mating systems. Under the conditions of this experiment, inbreeding did not aid selection.

It is perhaps most interesting that the cross of selected inbreds (M_{it}) only ranks in the lower level among other selected mating systems. Unfortunately, because of other uses, the M_a, M_r and M_d subclasses were not crossed.

The crossing of random-selected inbred replicates (R_{it}) exactly restored what had been lost by inbreeding. Significant improvement resulted from crossing the replicates of the random-selected random-mated subclass. Selection did not increase the amount of heterosis obtained in crossing inbred subclasses, but it did enhance net merit. The single line-cross available from the many full-sib lines started is no better than the random-random subclass.

Although this experiment did not involve a search for elite line-crosses, it does expose some of the weaknesses of the inbreeding system even for a litter-producing animal. Each of the other mating systems produced an equal or better result much more simply and efficiently than did inbreeding and crossing for a highly heterotic trait.

Other results of inbreeding and line-crossing in the same and different laboratory species are also presented.

Inbreeding is a valuable tool for certain experimental purposes but its value for efficient livestock improvement appears to be grossly over-rated.

DR. COCKERHAM: In what way did your results differ from what you would expect?

DR. KYLE: I think the cross of the selected inbreds I perhaps would have expected to possibly be at the highest level of any of the groups.

DR. COCKERHAM: Well, actually I guess I didn't stress this point this morning, but if you take a non-inbred population and make a group of lines without selection and then cross them in all combinations, what essentially you do is to recreate the non-inbred population.

And the success of the hybrid procedure doesn't really depend in any way on heterosis or inbreeding procedures but, rather, on specificity of genotypes that you identify and can repeat.

The inbreeding depression and so forth comes in in terms of what your chances are of coming up with the lines and so forth.

Also, deleterious genes more than likely will be eliminated so that crosses of the lines will give you an average hybrid performance probably a little bit above the original population.

But the success of the hybrid procedure depends on having a lot of lines, identifying good genotypes, and being able to repeat them, and doesn't depend on heterosis.

DR. KYLE: Well, I'll turn that around. Would you say that inbreeding and hybridization would work on a completely additive gene system?

DR. COCKERHAM: Yes.

DR. KYLE: In comparison to selecting in a non-inbred, say family?

DR. COCKERHAM: I wouldn't say it's the most efficient, but it works, you see.

DR. KYLE: It will work, you see. It won't be the best. No, I agree. I don't think it has to depend on the heterosis, but if you don't have non-additive gene action you can't expect heterosis, and to be efficient as a system to use inbreeding and hybridization you must have inbreeding depression and heterosis when you cross. Otherwise there is no point in looking at an inbreeding and hybridization system.

DR. COCKERHAM: That's right. To be efficient. And, of course, you do have inbreeding depression.

DR. KYLE: Yes, very much so.

DR. COCKERHAM: Now, if you can make the lines, you see -- and we look over the various groups that have done it in corn and so forth -- you can get initial response from this in terms of identifying good genotypes. If you can develop enough lines.

DR. KYLE: Right.

DR. COCKERHAM: So that you can have selection.

DR. KYLE: Yes, I agree. I'm just wondering whether, even if you could develop many, many lines in livestock, that would be the most efficient procedure. You can't develop and maintain that many. And even if you could develop an infinite number, I don't think this would be the best place to put that much effort.

DR. COCKERHAM: Yes, I quite agree with you. This depends upon whether you can develop the devices to do this.

DR. KYLE: I think it would work under optimum conditions.

DR. COCKERHAM: Maybe you can with ova transplants do this with some of your larger animals. But it does depend on techniques.

And, Dr. Sprague, I hear you are not going to be here tomorrow. One of the most successful people in this area has been Glenn Burton in terms of putting out hybrids involving all kinds of species, and generally in every case he has had to devise or invent techniques, which makes the development of lines or the crossing procedure or the production, putting the seed, so to speak, whether it's cuttings or what not, into people's hands -- Well, it requires a whole combination of things.

DR. KYLE: I also think if you can make a little producer out of a cow that you could improve her other ways as well. This would help not only inbreeding and hybridization but it would help on the selection methods also.

DR. COCKERHAM: This comes into efficiency.

DR. WILSON: I think we have discussed terminal tests in the laboratory and analysis such as the information you have here. But getting back to your initial statement that this was simply a hit-and-miss procedure, it just seems to me we're rather wasting our time to discuss what to expect if you put a couple of lines together in a laboratory.

You could expect anything you get, whether it's good, medium or poor, when you put two lines together. You could expect anything.

And I just don't think we can say from crossing a couple of lines or three or four or five what we are going to expect.

DR. KYLE: In a sense this is a population of sublines that you are talking about here which would be similar to -- from the same base population I think.

DR. WILSON: In a sense it's not population of sublines, because he never could keep all of them.

DR. KYLE: Not as far as full sib inbreds. This is true.

DR. WILSON: And the co-variances between those things, between a lot of those matings, is rather low, and this held the inbreeding down.

DR. KYLE: It didn't get as high as we had originally expected because the more inbred matings simply didn't produce offspring. We had to take offspring from less inbred matings.

DR. WILSON: So again these lines are not autonomous and are not separate lines.

DR. KYLE: No, not entirely.

Ralph, did you have a question?

DR. COMSTOCK: I want to make one comment about what you said with reference to Bell's experiment, because this always stuck in my craw.

Bell reported, and I think this you said, in generation 16. I think this was also at generation 30- something in his second experiment.

DR. KYLE: It was carried on to 39.

DR. COMSTOCK: He had a hybrid of inbred lines that was as good or better than his hybrid from crossings with reciprocal selection populations -- leaving then the inference that you could do as well with the inbred hybrid system with a lot less work than you could with the reciprocal selection.

Now, that conclusion might be correct, but I think it's wrong to infer it from his data, because if you look at his plot of progress in the hybrid and reciprocal selection, it showed steady progress right along, linear advance. It hadn't stopped. It hadn't flattened off. He just decided to stop. There's no way of knowing from his data how much that could have gone on improving.

And there's nothing from his data to say how good a hybrid he could have gotten if he had now developed some inbred lines from his two reciprocal selection populations and tried crossing between them, the sort of thing Clark suggested as a combination between the two things.

DR. KYLE: After reaching a point, then developing lines there? Yes, this would have been a pretty good approach.

DR. COMSTOCK: Continuation of reciprocal selection or the other could have taken him we don't know how much beyond.

So I think it's all wrong to infer from his data and I don't want anybody to go away with the idea that Bell demonstrated that you can do as well with the inbred hybridization system as you can with reciprocal selection because he didn't demonstrate it.

DR. KYLE: Well, I think that he would likely say -- certainly I would -- that in terms of animal breeding in livestock that if you haven't gotten it in 39 generations, forget it.

DR. COMSTOCK: Well, now, if you're going to take this, then you can say some things that you can't say otherwise. This raises some philosophical questions about whether we set up breeding programs for our grandchildren and so on, which I won't argue.

DR. KYLE: Don't misunderstand me. I'm not too happy with that. I don't think it works out that way in most livestock breeding. I doubt that hardly anything you do can be easier than inbreeding and hybridization than almost any other thing you can do in actual practice.

DR. COMSTOCK: I didn't follow that.

DR. BAYLEY: Neither did I.

DR KYLE: In other words, I don't think inbreeding as a system is ever going to be easier to reach a point with livestock, large animals at least, non-litter producing ones, than other systems.

DR. COMSTOCK: I wasn't prepared to discuss it with respect to livestock. Just with respect to Drosophila. And the fact that I think the inference that is loosely made from his work about it, useful as his work was, is a wrong inference and shouldn't be made.

DR. KYLE: This is quite possible. And I think it may be a special kind of trait in terms of the nature of the gene action involved.

Some of the other things that came out of that work indicated that; for example, the very quick plateau he got a little later in one set selected for fecundity made it look much too simple or special.

DR. COMSTOCK: I had a question I wanted to ask you. You spoke of significant differences between values that you put on the blackboard. What kind of an error term did you use?

DR. KYLE: This was a pooled within error across the different systems and I realize that had certain difficulties to it.

DR. COMSTOCK: You didn't use a rep by treatment error?

DR. KYLE: No, not on this one. This was the Newman Keuls test. I frankly think before publication we are going to revise both the kind of test and the way the error term is constructed for this.

You would prefer a rep by treatment interaction?

DR. COMSTOCK: Well, yes, because if you do a population by one procedure, the next time you do it the line may not go in the same place, and, in fact, in your two reps it didn't. In the first rep there was quite a spread.

DR. KYLE: But also in practical terms it was not possible to use a rep by treatment because there was none on the terminal test, you see.

DR. COMSTOCK: Yes, but you see, then, it isn't right to stand here and say that this was a significant difference if, in fact, the probability that you base this on is not the probability that applies. And I don't think it was the probability that applies. I think it's wrong to say it.

Because, here you talk about something that people can say: "Well, I can do that." This outbreeding, mass selection system. And you said it gave a significantly better result. And I challenge the statement, whether you had the basis for the probability test that you implied.

DR. KYLE: You don't like the error term then?

DR. COMSTOCK: No.

DR. WILSON: In another experiment with a different trait which was a little more heritable, larval weight and pupal weight, I did use the interaction as an error term and didn't find significance. It was about double the heritability in this trait. And I simply ran the regression of means and generations, took those regression coefficients, and put an analysis of variance on this and used this interaction for error term and did not find significance.

DR. KYLE: But that is a completely different trait.

DR. WILSON: To an extent.

DR. KYLE: Okay. Would a significant difference of regressions -- over generations -- Would you accept that?

DR: COMSTOCK: No: You see, the issue is: What is the probability that if I do this, make this comparison again and again, that the treatment that I said was significantly best would come out the best on the average in repetitions of the whole thing?

And it seems to me you can't make a statement about that probability. That is the one we're concerned with. We are concerned with the probability that if I go out and do this mass selection outbreeding that I will get a better result than I would --

DR. KYLE: You're really saying if I do it three times it won't come out the same as it did twice, and if I do it four it won't come out the same as it did on three. You'll come closer to approaching the parameter.

But I still say you can say, "Well, it came out this way this time, and this is the difference that showed up," and you can make a probability statement on these two times.

DR. COMSTOCK: But you should make it clear to what your statement applies. Your statement applies to the fact that the lines that you indentified here as a particular kind average better in their performance than some other lines, without implying that if you used the same system again that the systems --

DR. KYLE: Oh, right. Your interpretation of results. Okay. This applies to this experiment. And not reach out very far as to what would happen in others. That's what you're objecting to. Okay. For a different trait it might be completely different gene action.

DR. COMSTOCK: No, the same trait.

DR. KYLE: For the same trait again?

DR. COMSTOCK: You had two reps.

DR. KYLE: Yes.

DR. COMSTOCK: Therefore, you have a basis of test --

DR. KYLE: Yes.

DR. COMSTOCK: -- of the difference. It's a kind of important one. You say if you have three, four or five then your test becomes powerful, and if you get the same result every time you can say significantly so this happens and will continue to happen and therefore it is a fact.

DR. KYLE: Somewhere I've been lost here. I think that the difficulty comes in reaching out to try and make the comparison between the two reps of generation 8 and the terminal test results. And I can discuss this another time. But as far as having the material to test at generation 8, we have it. Okay?

EXPERIENCE IN SMALL MAMMALS

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Well, I had a hard time deciding what I ought to include in this talk, so I obviously think under those circumstances one has a hard time to get his talk prepared. But with all the fun we've been having, I'm not too dismayed at this point.

Just starting off, I would like to question the procedure that was followed by Wendell Kyle. I just wondered is it decent to go right to the heart of a matter and settle it once and for all before the thing has been decently "conferenced"? He sort of took a little of the "what happens next" out of it.

I agree with him on an awful lot of what he said. I could argue about, oh, some of the details of his rationale here and there. But with the trouble we have reaching understandings in this world anyway, I'm not sure whether that's worthwhile as long as we agree on the conclusion.

Now, I'm not going to offer a very spectacular talk. At least to my mind it isn't. I have this assignment of experience with small mammals. I don't have much personal experience with small mammals. I can't draw very heavily on that.

So it seemed to me that perhaps the best I could do was to take a bit from the literature that reflects on the problems that are encountered in connection with inbreeding and cross breeding in livestock.

Now, it is a little discouraging, because, in view of what Wendell said, we're just spinning our wheels and beating our gums here, because he's got it decided.

Before I go any further, I want to just sketch a few issues that seem to me to be pertinent to what we're talking about.

One of them that hasn't been mentioned is that we have no animal breeding programs in which the scope of operation is what it ought to be. This is one of our problems all the time.

Whenever we talk about ways of proceeding in livestock breeding, we have to be very cognizant of the fact that our operation that we propose is not of a scope that goes beyond the facilities or cooperation that can be made available.

Let's see. I think somebody -- who was it? -- this morning said if you're going to inbreed you ought to have a reason for it. And we could dwell on that point just a little bit. I'll just make an assertion or two.

Well, one of the assertions that I have to make first is that I'm not completely sure of my ground. And I'll put forward a couple

of things tentatively.

We say that the procedure in breeding should depend on the mode of gene action. We can see some connections between the nature of inheritance and the genetic mechanism and the systems of breeding and selection that ought to work.

And in this connection the only thing that I'm real sure of or that I'm most sure of is the thing that Sewall Wright said back in about 1938 -- that if you had a great deal of non-allelic gene interaction it would be useful to develop inbred lines and select among them.

Now, there would have had to be some qualifications put on this, because this gets you into this other problem of scope of program relatively rapidly. Because you develop a bunch of inbred lines and perhaps pick a smaller number that are the best of them and then intercross them and start the whole thing over again.

And there are some restrictions in connection with inbreeding or genetic drift, whichever way you'd like to talk about it, such that if you're going to go very far with this sort of thing you have to start out on a pretty large scale to begin with and have to have pretty ample facilities to keep the thing rolling.

Now, there is another thing that I want to throw in the hopper in connection with why you might inbreed. There was a little discussion just before lunch on the desirability of it, the utility of it, depending upon the amount of dominance or non-activity.

And it was agreed between Dr. Cockerham and Dr. Kyle that if everything were completely additive, still you could make progress by developing inbred lines and selecting among them. And there was some question about the efficiency.

There is something else that ought to be inserted in connection with this, and that is the cost of making the phenotypic observations you want to make, the cost of making the evaluations that you would really like to make.

In general inbreeding programs we get awfully skimpy on the measurements that we use as a basis for selection. In my professional career in breeding swine, I have had a great tendency to want to select on the basis of growth rate because it's awfully easy to measure and you don't have to wait a generation before you make evaluation.

Things get troublesome when you have to go farther in carcass evaluation than a back fat probe, because you have to do it on a basis of relatives, sibs, or something like this, and it gets expensive.

We see in the literature things about heritability, about palatability or tenderness or marbling, and this seems to imply to me that somebody is interested in the possibility of selecting for these things so that we have better meat. And, of course, you can't

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[illegible], about

do much of a job of that if you're going to do it every year on a whole bunch of individuals.

But if you are developing inbred lines, it is a fact that after you have a line at a high state of inbreeding you might then go to the trouble of evaluating your lines with respect to some of these things that are costly to measure.

I recall Dr. Hayes out at Minnesota emphasizing this as a big advantage of the inbreeding system for corn, that you could develop a line at relatively little expense and you didn't have to worry -- about making observations on it, just go ahead and develop a bunch of lines and make a lot of crosses and then do all your evaluation at the level of crosses or lines, as the case might be, and sidestep an awful lot of work of evaluation that would be involved in a selection scheme that was recurrent over a shorter time interval.

And I think there is actually something to be thought about in this connection, because in livestock breeding we do shrug off and sidestep some of the things that are important to us but which are really just impossible to measure often enough and on enough individuals to incorporate it into our standard mass selection breeding procedures.

You can think of, besides the things I mentioned, things like resistance to one or more diseases, which is just impossible to measure at the level of individuals year after year.

Well, one of the other things that I think I ought to make a statement about -- you probably all recognize it -- is that we have an entirely different problem in livestock than we have in corn. Wendell Kyle really was aiming at this.

We got all excited about inbreeding and cross breeding, or more excited, as a consequence of success with corn and kind of forgot that for the same amount of money you could develop thousands of homozygous lines of corn where with livestock the same money would give you a handful of lines and perhaps not inbred to the same degree.

Some of the things that I tried to keep in mind as I looked at a little of the literature on small mammals are the following things:

First, what is the evidence with respect to the degree of inbreeding depression? This is pretty important. Of course, we have this information from livestock so we really wouldn't have to get it from small mammals. But I guess I'm looking at it just from the standpoint of comparative interest now.

It is an important thing, because if there is going to be a lot of inbreeding depression this means the cost of developing lines is going to be a lot greater.

And we have sometimes, some of us -- I don't want to incriminate anybody -- tended to say that if there is a lot of inbreeding depression there will be perhaps a lot to gain in hybrid vigor. In

other words, viewing the two things as the opposite sides of the coin.

But Jim Crow expliained to us back in the early '50's that this isn't the case, that you can just get all kinds of inbreeding depression as a consequence of making homozygous rare deleterious genes, and that going the other way and covering up these with their dominant allelomorphs the things you accomplish by cross breeding may then gain you only some relatively small amount like five per cent.

So that it seems to me the intensity of the inbreeding depression is important to us in terms of cost rather than the matter of guaranteeing that there is something to gain by going the other way.

We'd like to know, if we could, from the inbreeding and cross breeding data or anything related to them something about the level of dominance and, in particular, whether there is an important amount of overdominance.

This was, of course, touched on by Dr. Sprague this morning, and he summarized a lot of experimental work in corn by saying that at the present time there is no strong evidence for very much overdominance in corn.

There is a sort of rule of thumb -- I don't know whether you call it that; let us say a scientific argument because it sounds better -- that the direction of dominace which is important to us in connection with this business that we are talking about is a function of past selection, that we expect to find favorable alleles dominant in cases where there has been a history of past selection in one direction.

And this seems to be borne out. This, of course, goes back to Fisher's writings on evolution of dominance. And we generally, many of us, invoke this idea to explain the fact that reproductive traits seem to be more heterotic and exhibit more dominance than some other traits. And this is a matter of some interest.

And then, finally, it seems to me there is some interest in what we would predict as a consequence of mass selection or other intrapopulation selection schemes, again as a function of past selection.

Dr. Sprague showed us the slide showing the remarkable success of Dr. Gardner in mass selection within the Hays Golden variety of corn. And he could have, I thought, given some other example of success of this kind of selection in corn that he didn't give.

But, at any rate, one can raise the question of whether there really has been a very long history of selection, efficient selection, for yield in corn, -- a history of selection that would have suggested that any kind of genetic variance should be exhausted,

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But Jim Crow explained to us back in the early 1950's that this isn't the case, that you can just get all kinds of inbreeding depression as a consequence of making homozygous rare deleterious genes, and that going the other way and covering up these with their dominant allelomorphs the way you accomplish by cross breeding may then gain you only some relatively small amount like five per cent.

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and then attached to that idea perhaps the idea that in corn the environments have changed.

Not knowing anything about corn, it seems to me that the environment has changed quite a bit, that fertility levels under which people raise corn and planting, spacing, the number of plants per acre, and so forth, have been increased. And this places corn, commerical corn, in an entirely new environment and one for which there hasn't been selection for more than just a very short period of time.

I don't think it would be decent in talking about small animals relative to inbreeding and cross breeding if I didn't start with the guinea pig work in the Department of Agriculture that was reported so carefully by Sewall Wright in Bulletins 1090 and 1121.

And I think the evidence there is some of the more interesting evidence, and really in lots of ways not very much has been added to it.

Now, I don't want to delude you. I didn't read those bulletins carefully during last week. I did skim through them, however, and I saw some things that I didn't see before.

I saw, for example, in one of these bulletins, that Sewall Wright paid quite careful attention to the issue of partial and complete overdominance. He didn't use exactly those words. He was talking in connection with over dominance in connection with the stimulation theory of East. And he pointed out in not such a long paragraph that this was really a critical issue relative to systems of breeding livestock.

Well, the philosophical issue is all laid out there. I'm not quite sure that everybody besides me knew that this was so or remembered it. How many of you are fully familiar with everything that is in that bulletin, remember all the results, and so on?

I'm going to put a few on the board with your permission. Most of the rest of the information that is available is on mice. And in a lot of the things that you read about mice the material is based on inbred lines, as Kyle pointed out, and the heterosis that you see when you cross inbred lines, as he noted, is not really quite what we're interested in. It indicates that there is some dominance, and so on, but it isn't exactly what we're interested in.

So I should point out that the foundation stock, of guinea pigs, that was used here according to the statement in the bulletin, did not trace to inbred material with outbred stock. They had a little misfortune one year and they got down to 54 animals, so they had a bottleneck of 54 animals in 1897 and then apparently increased the size of the stock.

I remembered after I read it again that there weren't really very many inbred lines. Actually it started out to develop approximately 35 lines by full sib mating. And 11 of these were lost almost immediately. Twelve of them were lost almost immediately for reasons not connected to the inbreeding, according to Dr. Wright. They were lost before the second generation, primarily because a single female didn't produce enough live offspring of both sexes.

Then they lost four more lines before 1915, which was about 11 years.

I mention this in connection with the one aspect of developing lines that you always lose lines. They didn't really lose such a large proportion in this particular experiment.

Finally, they reduced the number of lines to five on the basis of the performance of the lines. Cross breeding work was done using those five lines.

Just to remind you, they had about 18, it's more or less fair to assume, out of 23 lines that survived for about a ten-year period, which roughly meant six to eight generations of sibbing the way I interpreted what was written.

This I have to write up here (at the blackboard). Well, those of you that read the papers recall that the data were compressed into lots of characters. There were a lot of characters for which results were given. And I just selected four that I thought would suffice -- litter size, young per year, percent raised of all born, and weight at 33 days.

What I'm going to put down now is what he gives as the regression equations on time. And this doesn't convert directly into regression on inbreeding, so I'll have to explain just a little bit then. And I can only do it roughly.

Now, "X" is the number of years after 1906. And I'll just say that this ran out to 1916 approximately, the data on which he used this. That covered the period during which most of the lines were there. And so that was about ten years. And about eight-tenths of a generation per year more or less. So this is perhaps eight generations of full sib mating.

And how much inbreeding did he get in eight generations of full sib mating? Do you remember? Do you remember, Clark? Eighty percent?

DR. COCKERHAM: Somewhere between eighty and ninety I guess.

DR. COMSTOCK: Let's just say 80 percent. All you have to do is say, well, if I multiplied this by ten I'd get -- Let's see. If I multiplied that by -- what? Darn me! Yes, if I multiply it by ten, then that's about 80 percent of the depression.

So you see this comes up .043, and the inbreeding depression doesn't look very great relative to the average litter size at the beginning. This is the point I want to make. This is really so for all -- At least it's so here.

If you multiply this by ten, it gets to something that is over a third of this. That's young per year, and that's a composite of litter size and number of litters per year. And then here the liability you might say. Multiply this by ten, and it still doesn't get very big relative to this.

And the weight you're all going to guess isn't going to be very big, and you'd all be right.

Well, that just in general shows that if you can forget about the lines that were lost -- there were four of them there -- that inbreeding depression really wasn't terribly great in the guinea pigs.

DR. HODGSON: What was the degree of inbreeding?

DR. COMSTOCK: This was ten years. I have just approximated that it would have been about 80 per cent that time. So that would be when most of the depression would have happened.

DR. KYLE: What's the mumber of lines involved in that?

DR. COMSTOCK: Nineteen.

DR. KYLE: Four were lost?

DR. COMSTOCK: Now, remember it is true at the beginning there were 23, and as near as I can tell there would have been a little bias here because there were four lost along the way.

DR: KINCAID: They had 35 and lost 12 right quick, which left 23, and only four more went out?

DR. COMSTOCK: That's right.

Now, if we just put a few figures down here to get a general idea out of what he got out of crossing, these are the average of the inbreds. And these were first cross. Of course, there were inbred dams here. No increase in litter size. No increase in young per year. A bit of increase in per cent raised which you'd expect. And some increase in weight at 33 days.

Now, these are double crosses which you get to the case where you have cross bred dam as well as cross bred offspring. And there wasn't much gain here (litter size). There was a lot of gain here (young per year) because they just produced a lot more litters per year. And there was a gain here (per cent raised). And some here (weight at 33 days). And I think you'd expect this too because this

[illegible] mean score up .023, and the inbreeding depression [illegible] very great relative to the average litter size at the [illegible] is the point I want to make. This is really so for [illegible] it's so here.

If you multiply this by ten, it gets to something that is over a third of this. That's young per year, and that's a composite of litter size and number of litters per year. And then here the livability you might say. Multiply this by ten, and it still doesn't get very big relative to this.

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DR. [illegible] What was the [illegible] inbreeding?

DR. [illegible] This was [illegible] I have just guessed that it would have been about [illegible] per cent that time. So that would be when most of [illegible] would have happened.

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DR. KINCAID: They had 35 and lost 12 right quick, which left 23, and only four more went out?

DR. COMSTOCK: That's right.

Now, I [illegible] put a few figures down here [illegible] get a general idea out of [illegible] got out of crossing, these are [illegible] average of the inbreds. [illegible] these were first crosses. Of course, there were inbred dams [illegible] increase in litter size. No increase in young [illegible] increase in per cent raised which you'd expect. [illegible] weight at 33 days.

[illegible] able crosses wh[illegible] to the case where [illegible] inbreeding. And there [illegible]

is weight at 33 days, which is a weaning weight, which depends on the vigor of the dam to some extent.

Now, because of this figure I'm going to go back and put another one down here. This was a threeway cross with a cross bred dam. And there for some reason these two didn't really jibe (litter size). These cross bred dams did do better. And that figure is more or less the same (young per year). This one (per cent raised) is up some more. And this one (weight at 33 days up a bit.)

Now, to put down outbred controls, 2.65. It went up here from the outbred control, (litter size). There was some of that real animal husbandry heterosis here. And there was some here (young per year). There was some here (per cent raised). And a little bit here (weight at 33 days).

I could go on and put down some more numbers. I don't think I ought to take the time. I could put down what the performance of the best inbred line was.

The thing I can say is that the best inbred line out of these was not as good as the outbred control, and they were choosing one line for one trait and another line for another trait depending on which was a different trait, so the inbred weren't just as good.

I'll put down one more set of figures. Here this represented a population in which he just out of cross breds selected good individuals wherever he found them and mated them, so that he had a population that was selected for growth. These were selected for growth out of any cross no matter where they occurred.

And this is a pretty decent figure (litter size). This is the highest in this row (young per year). This is a pretty decent figure (per cent raised). And this is the highest in this row (weight at 33 days).

And this I think had something to do with a conclusion that Wright came up with about livestock breeding procedure that I suspect has influenced the course of livestock breeding a great deal.

Now, before I go to that, let me just throw out a little summary that I had planned to make. Cross breds were better than the control. Best inbred was poorer than the outbred control. And they got the best performance when the dam and young were both cross bred.

Well, that's all old stuff to you.

Now, Wright made some statements about the meaning of this information. Wright made some statements about what this would mean for livestock breeding. I'm almost tempted to read it verbatim, but I'm not going to. I'm going to try to paraphrase.

He said that the heritability -- in effect he said that --the heritability of gain in litter size was slight and less than ten per cent, and, as a consequence, he said, the routine systems of selection would be very ineffective and that they'd be risky, that at any time an unfortunate choice of sire might wipe out the progress that you had made prior to that.

In contrast he said that in essence that selection among inbred lines followed by crossing yields progress not to be attained by selection alone.

And looking back and not knowing anything about it, because I was awfully young at that time and don't remember too well, I suspect that these words had a tremendous influence in setting off a whole series of inbreeding programs aimed at realizing this advantage of inbreeding that he suggested and that Wendall tells us isn't there.

Now let me give you a little miscellaneous stuff. I don't know exactly why I'm giving this. It's just possibly because I think you might be interested. It does relate a little to this issue of whether heterosis depends on the direction of past selection in accord with a general genetic principle that we think holds.

So I'm going to give you something like eight or ten "quickies." Most of them are on mice, and until I tell you differently it will be mice.

A man by the name of Jan Bruell just this past year reported on wheel running. And I assume you know what wheel running is as well as I do. He measured it in 13 inbred lines and 31 crosses.

I happen to know Jan Bruell. I think he probably did a pretty good job. He's that kind of person.

He says that there was a significant proportion of the F_1's that displayed heterosis for wheel running, and he says further that the crosses of completely unrelated lines showed more heterosis than the crosses of lines that were in some way related though not necessarily very closely.

So there's nothing here that surprises us except possibly that wheel running is a heterotic character.

Now, you might ask: Were mice ever selected for wheel running in the past? Well, they might have been selected for agility and running, if not on wheels.

A young man at Minnesota by the name of Winstom, whom I happen to know, looked at three lines and the F_1 crosses of them in terms of water escape. He throws them in a tank and sees how fast they find a way to climb out. There is a way.

And infantile trauma. He exposes them to some kind of shock when they are young and sees if this blights them for the rest of their life.

And maze-solving.

Now, what he says is that the F_1's were significantly superior in water escape and resistance to infantile trauma but that the results were not conclusive for the maze business.

There is a Polish gentleman whose name I can't pronounce -- if anyone is interested I have the spelling here and I will give it to you later -- who crossed some strains of mice and then extracted two inbred lines and also an outbred strain and found things that don't surprise us very much with respect to components of reproduction.

I'm going to give you now the ratio for outbreds as compared to inbreds:

Eggs ovulated, 1.10.

Eggs fertilized, 1.33.

Eggs implanted, 1.46.

Living embryos, 12-day, 1.68.
Number born alive, 1.77.
No real surprises here.

Here we have one on nest building and gnawing (Barnett and Scott). Four lines and the crosses. They discovered that the crosses were heterotic for intensity of gnawing and efficiency of nest building.

Now, there would have been natural selection for those in the past, wouldn't there?

No heterosis for general activity in whatever way they measured it. I don't think that means much because I don't know how they measured it.

A Japanese gentleman by the name of Mori took a look at per cent of abnormal sperm. Two inbred lines in F_1. One inbred line, the per cent of abnormal sperm 9.4, and the other 28.8. In one of the reciprocal crosses, 4.7. The other reciprocal cross, 5.7.

So heterosis for per cent of abnormal sperm.

Heat tolerance. Here's one on heat tolerance. F_1's usually had more heat tolerance but not always he said. However, inbreds adapted better. I don't know what you make of that. I'm not going to try to make anything of it.

Some other people measured heterosis in two temperatures, 21 degrees Centigrade and minus 3 degrees Centigrade. They found that the heterosis for reproduction was greater at minus 3. In other words, the inbred mice did a bit better. The crossbred mice, I mean, their reproduction wasn't harmed as much by the low temperature is what it turned out.

For example, young born per pair, the crossbreds went down from 44 to 28, whereas the inbreds went down from about 30 to about 10. That sort of thing.

Now, here is one on another species. This is on mink. The gentleman Johanseen of Sweden said he didn't really have much data and you shouldn't take it too seriously. But what he found was that the number of kits that survived in third matings, full sib matings, had gone down about to 1.1. It started at 4.3. And the November weight of kits went down about one-third, about 33 per cent.

He made cross matings, and in the F_1 where the female was inbred he didn't get much increase in the number of kits surviving , but when he made the double crosses, lots of them, 5.8 surviving, and he recovered a lot of his November weight.

So he said, "I don't know exactly what this means for mink breeders, except don't inbreed".

Now, one of the other bits of information from mice, mammals, a different kind, down at North Carolina. They conducted a relatively extensive experiment with mice to estimate the non-additive genetic variance. Dr. Cockerham was involved. He's one of the authors. So if I don't get it right, he will correct me. This is Miller Legates and Cockerham.

They used a design that gave them an estimate of something like a quarter of the dominance variance, and in the case of measures of growth, weight at three and six weeks and gain from three to six weeks, they didn't find any. In litter size this amounted to seven per cent of the total. So if you multiply it by four, I guess this would be 28 per cent of the total variance.

A suggestion that there is some non-additivity, which is no surprise either.

Now, I am next going to give you a few results from Falconer's group on litter size in mice. The character that they used was size of the first litter, which may not be the best character to use, but it's the quickest to get data on.

In a paper by Roberts in the first issue of Genetical Research, he started off 30 lines to be full sib mated for three generations. He started these off from Falconer's populations that had been selected high and low and the control population in his selection for litter size experiment.

He lost four of the lines, two for reasons not connected to the breeding. Again we have this business of line loss even though you are only going to 50 per cent inbreeding here. He lost a couple out of 30.

And then he made a set of random crosses within each set of lines. There were ten lines from each of these sources, the high population, the low population, and the control population.

And he made a set of ten crosses in replicate from each of these groups and then another ten crosses not in replicate, so he was planning on about 30 litters, really, if I read his paper right.

And then after that he did double crosses in more or less the same pattern. And I'm just going to take a moment to write these results up here.

At generation zero, first inbred, second inbred, third inbred, and first cross and double cross these will be. And we're interested in the average litter size. At zero, 8.12. There aren't really going to be any surprises here so don't be looking for them Then 6.73, 5.82, 5.69, 6.20 and 8.47.

One of the things that I think is interesting is that there wasn't really a terribly drastic inbreeding depression as far as litter size was concerned. This was with dams inbred 38 per cent and offspring inbred 50 per cent. And they have gone down about two and a half. And maybe if you went all the way to homozygosity you ought to expect two and a half to three and it would leave you something.

And you could ask yourself whether there has been strong directional selection for litter size in mice in the wild and you might come up with the answer that perhaps not, perhaps there is an optimum litter size rather than a maximum that is desirable.

Well, the main point that he made was a point kind of like Wendall's — that this wasn't any higher than this, that the line crosses didn't do any better than the original outbreds.

Now, he did recognize that wasn't really the issue. The issue would be whether you had variation among these crosses so that selection among the crosses could give you something better. And his analysis didn't reveal a great deal of variation. I'll just leave it right there.

I'll say that his analysis didn't have very many degrees of freedom and didn't give very accurate estimates.

I might also say that I frown on making a comparison between meanings that were obtained in certainly different years and different environments. And he himself said this is only 3.5 larger, and these means in essence, he said, bounce all over the map, so you can't take

that 3.5 very seriously. And he concluded that there wasn't any increase.

Now, Bowman and Falconer also published a paper just about that time. They had in essence an outbred stock. They didn't go back to inbreds. They started off with 20 lines, ten lines in which they were doing some selection and ten lines in which they were selecting within lines but admittedly the selection wasn't very strong. But at any rate they made the comparison.

And it turned out selection didn't do them any good. They lost more of those lines than they did of the others, and it didn't help any. Three of the lines in the first set survived to generation ten and then two more were lost. They had one line that survived indefinitely. And this line showed no inbreeding depression in litter size.

This they made quite a point of when they say this indicates that overdominance can't be of really special importance.

I would say along with that they wouldn't be right to conclude there wasn't any on such basis as this, that such a line with many -- if there were some over dominance loci but some others as well, and we would be pretty sure there are some others as well.

Well, now, I have got another little set of figures here that I guess I'll put down perhaps for emphasis. They found the inbreeding depression here -- They estimated it at .56 per ten units of F. So extrapolating to 100 per cent inbreeding, that would mean a loss of 5.6 mouse per litter. And they started off in about the eight range, so they would have ended up above ground, let us say, except that there seems to be something else because of this loss of lines.

Now, you lose some lines accidentally because you just don't provide yourself enough insurance, and you get a couple of small litters, and the sex ratio goes a little awry and some mouse catches a cold and the first thing you know you're out of business.

Well, here is the main thing I wanted to put down. This is generation, and this is 8 in the first go of inbreeding. 6.08 is average litter size. Then cross went up to 7.53. And double cross went to 9.58. And I forgot the exact figure I must say and I didn't write it down, but something like 8 for the benchmark, the outbred control.

He then took his crosses, interbred them, started inbreeding them again, another set of 20 lines. He got generation 4, just did it for four generations. Inbreeding depression again 6.89. Crossed -- Here is where you hope that you go up to 12 or something, and he went up to 7.8. And double cross, 7.9.

He did it again, four generations of inbreeding. 6. Cross, 6.8. Double cross, 7.3.

So his successive cycle were disappointing. And he pointed out that you could explain this in terms of the inbreeding, that the first go-round he selected three lines so you only had really three gametes, and the next go-round he selected four, so the inbreeding coefficient even on the double crosses at the end I think was some 40 per cent.

Here are the inferences he made:

That selection within lines was ineffective. And there seemed little doubt of that.

That the absence of inbreeding depression in the one surviving line implied that overdominance was not of really grave importance.

And he really concluded that the failure to improve in the second and third cycles demonstrated ineffectiveness of cyclical inbreeding and crossing.

And, of course, here you can raise a question. Well, if you did it on a bigger scale so that at each stage you could select a larger number of lines so that your inbreeding wouldn't go up, what then?

There are a couple of other things that I could give you but I'm not going to because I do want to stay within my time as long as we started late.

I do have experience, just a little bit of my own that I think might be germane. We have a selection experiment at the University of Minnesota. Selection is for post-weaning growth. The population was initiated from the cross of just two inbred lines. Selection just for that one trait. The selection has been effective. We are in the 28th cycle of selection now.

The response to selection has been almost linear. Statistically you can't detect any non-linearity on time. So there is no evidence of a plateau.

The interesting thing in connection with what we are talking about now I think is the things that happened to litter size, because reproduction is so important in connection with our inbreeding and crossing.

The selection for growth has given us a correlated response in litter size. The litter size has been going up about a tenth of a mouse per generation, so it has actually increased about two and a half mice since the outset.

Now, I'm sorry to say that I don't have data on what the F_1 was -- or possibly it should be really the F_2 level. That would have given cross bred dams and cross bred offspring. I couldn't tell you what the F_2 level was. The F_3 level was about six mice. And we're now at about eight and a half.

You can imagine that the F_2 might well have been somewhat above six. But I'm guessing that we have gone out beyond the highest that we got after the cross, and there was a fair amount of heterosis. The lines themselves give about four mice per litter.

So what this says is two things. It says not all the genes are overdominant. It says not all the genes are completely dominant. It says those things for sure. And it leads you to suspect that there are more that are partial dominant than otherwise.

Well, I have a line here that says "General Summary." I've kind of forgotten when I wrote that, so I kind of hesitate to read it, but we'll take a chance.

What I see from the somewhat cursory review of literature on small mammals is there is relatively little inbreeding depression for growth. That doesn't surprise any of you.

There is more inbreeding depression and a moderate, fairly considerable amount for litter size, number of litters and survival. This doesn't surprise you.

There is always a loss of lines, but some come through that are almost as good as the random bred stock.

Now, the fact that there is a loss of lines doesn't surprise you. I doubt if you are surprised at the fact that with these you can bring some lines through.

You might be a little surprised to know that these lines may be then pretty good performing lines such as they were with Helen King back in the old days with rats.

And I want to add from my own experience that in mice the hybrid level can be recaptured and transcended by just straight-out intrapopulation selection.

Well, that's my story, whether coherent or not.

DR. WARWICK: Thank you.

Is there a quick question or two anybody would like to direct to Dr. Comstock?

DR. HODGSON: I'd like to ask a question. In your opening remark you kept referring to the question of scope. I think you

meant numbers of animals. And that means where do you put them. In doing some of these things and testing out lines, and so forth, what are you thinking of in terms of scope? What do we need?

DR. COMSTOCK: Well, in the first place, I want to go back to Wendell's statement. In the first place we need to be pretty sure that we think it's worthwhile. I really think this is the first thing.

After that I really can't quite answer your question, but it is quite a bit more than we have ever had available.

You see, I think, going back to my own experience in connection with swine breeding laboratory where they set out to develop a modest number of inbred lines of swine, in general the lines didn't perform very well in their own right. They kept getting a little poorer. The nagging question always was: Well, now, if we crossed these would we get more performance than we get out of crossing the the breeds? In other words, non-inbreds.

But there were never facilities to do this crossing on the scope it needed to be done.

Now, I can't quite answer the question of how much, but it takes a fair amount.

And the other side of this story that seems to deserves emphasis is that our time-honored methods, the selection within a closed population such as a breed or a smaller closed population such as a farmer's own herd, require least in the way of facilities, special facilities, and animals to do it at what is maxium efficiency for that system.

It is an unfortunate and sad thing, I think, that even this method of breeding and selection has never been done at its maximum efficiency and never close to its maximum efficiency.

DR. HODGSON: Well, on these facilities, can it be any place? Do you need concentration or not?

DR. COMSTOCK: I wouldn't say it was absolutely necessary to have concentration. By that you mean all your animals brought together in one place?

DR. HODGSON: Yes, or in a uniform environment as much as possible.

DR. COMSTOCK: No, there are ways of getting around that.

But one of the things is if you have them in one place, of course, you run the risk in one place as you all know of these disease problems, and so on. So I won't say anything about that. But if you

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You see, I think, going back to ... swine breeding laboratory where they ... modest number of inbred lines of swine, ... very well in their own ... They ... poorer. The nagging question always ... these would we get more performance than we ... the breeds? In other words, ... inbreds.

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It is an unfortunate and sad thing, I think, ... breeding and selection has never been done at its maximum ... its ... efficiency.

HODGSON: Well, on these facilities, ... concentration or not?

: I wouldn't say it was absolutely necessary ... By that you mean all your animals brought together

in a uniform environment, ... such as

getting ...

don't have them in one place, then you have problems of cooperation, and you have some disease problems then too, transferring diseases from one place to another.

Now, I can exemplify a little from our swine project at Minnesota. I could give horrible examples on the disease problems. I won't do that. But we do have a large integrated project that involves animals in six places I think, and the design and the way the places are used is such that I think we don't suffer very much from having the animals at six places and maybe gain something.

DR. HODGSON: Thank you.

DR. WARWICK: DR. Cockerham.

DR. COCKERHAM: I don't think you meant to infer, but I'd like your opinion anyway, Ralph: Do you think that you could improve on very highly selected hybrids generally by random mating and then selecting? Your last statement was in terms of your line crossings you really did better than the hybrid by family or mass.

DR. COMSTOCK: Well, let me --

DR. COCKERHAM. But that wasn't the selected hybrid, was it?

DR. COMSTOCK: No, sir; What I was thinking about there was that this hybrid contained all the genes that were available to the population in which we did our selection. So making use of the genes that were in the hybrid and making some of the good ones homozygous apparently, we were able to transcend the hybrid level of performance.

You had really a different question.

DR. COCKERHAM: That's right.

DR. COMSTOCK: Your question was whether if you developed a lot of inbreds, made all the crosses and picked the best you could transcend the performance of that by selection within a non-inbred population. And, of course, I don't know the answer.

DR. COCKERHAM. Yes, I just wanted an opinion.

DR. COMSTOCK: I believe the answer to be yes. This is partly conviction that you get after a while. I'm pretty sure the answer is yes because of the fact that your probability of getting the best that is in your genetic system in the best cross of even quite a lot of crosses is pretty remote.

DR. KYLE: I just wanted to make a point on the matter of scope. It may not be necessary to form selected populations say at the same place but eventually you would certainly want to test the best strain

crosses or crosses of selected groups at the same place to make your selections. And this would take large scope and facilities just as testing line crosses.

DR. COMSTOCK: Let me say one thing. In our swine breeding project we selected different systems of selection at different places, but we bring the material together at one place for the comparison of the results of selection at the cross bred level.

DR. HETZER: I believe in reply to the last preceding question you compared crosses with results you might expect from the development of interline crosses. I wonder how you compare those with reciprocal recurrent selection, which of those you expect the most progress.

DR. COMSTOCK: Well, of course, you're talking, you know, about the "woman I love." And it is an unfortunate fact that reciprocal selection is a hard system to run with livestock, and I don't advise anybody to use it unless they are pretty well convinced that this is the only way they can get out of the material what is potentially in the genes.

I have an entirely different recommendation for the corn people.

But it's a very heavy system, and at this stage I'm not shouting that you should use reciprocal selection by any means.

DAIRY CATTLE - Resume of Past Work

W. J. Tyler, USDA, University of Wisconsin

The effects of inbreeding in dairy cattle have been investigated by many workers. In only a few experiments were inbred lines developed to determine heterosis that could be measured from crossing inbred lines. Analyses on quantitative characteristics under different systems of mating were made mainly on three types of data:

(1) Inbreeding experiments. Due to limitations in experimentation with large animals, this type of data is relatively rare. The experiments have generally been started with one or few foundation bulls. By systematically mating, different sire-lines were developed. Inbreeding has been, on the average, higher than that found in the following two types of data. Selection has usually been practiced within or between lines. In some cases, contemporary control outbred animals from the same sire were available, although the number of both outbred and inbred animals was relatively small. (1,2,3,4,5,7,10,11,13,14,16,17,18,19,20,22,23,24, 25,29,31,32,34,37,39,40)

(2) Records from closed herds. In these herds mild inbreeding, or linebreeding, to a particular sire has been followed. The animals have been descendants of one or several related or unrelated foundation bulls. In general, average inbreeding has been low. Both selection and assortive mating of varying intensity have operated. (6,8,12,15,21,26,27,28,33,35,36,38)

(3) Herdbook data. The amount of inbreeding has been calculated in pedigree matings. The data generally represented a wide sampling of bulls in the population. However, both sires and dams have been subjected to selection. Therefore, the data are likely to represent highly selected animals. (9,30)

Under the conditions of the various investigations reviewed, intensity of inbreeding was relatively low and artificial selection was usually practiced for high production or other desirable performance traits. Several lines of evidence concerning the effects of inbreeding and outbreeding in dairy cattle appear to agree with findings in other species of animals.

(1) Inbreeding presumably increases the proportion of homozygous loci as shown by an increased incidence of recessive lethals in inbred groups.

(2) There is a general decline in level of performance as inbreeding progresses (See Table I).

(3) The closer the character is related to fitness, the more it is subject to inbreeding depression as shown by high mortality in inbred animals, particularly at early stages.

Table I

Influence of inbreeding on production traits of dairy cattle.

Investigator	Breed	Regressions of traits on coefficient of inbreeding b Milk	b Fat%	b Fat	Heterogeneity among sires
Plum - 1934	Jersey	Neg.			
Bartlett & Margolin - 1944	Holstein	Neg.	Pos.	Neg.	
Woodward & Graves 1946	Holstein	Neg.	No effect	Neg.	
Ralston, et al. 1948	Holstein			Neg.	
Swett - 1949	Holstein	Neg.	Neg.	Neg.	
Tyler, et. al. 1949	Holstein	-74	0	-2.3	Yes
Laben & Herman 1950	Holstein	-66	0	-2.0	Yes
Nelson & Lush 1950	Holstein			-4.5	
Davis, et. al. 1953	Holstein	-31	+.03	-0.7	Yes
Robertson - 1954	Friesian	-30			
Laben, et al. 1955	Holstein	-210	+.01	-4.9	Yes
Plum & Rumery 1956	Holstein			-0.5	
von Krosigk & Lush - 1958	Holstein	-54	0	-1.7	No
Hansson - 1961	Swedish R & W	-31			
	Friesian	-22			
Gaalaas, et al. 1962	Holstein 1st Lact.	-105		-3.6	
	2nd Lact.	-42		-1.1	
Brum, et al. 1963	Holstein 1st Lact.	-41		-1.2	
	2nd Lact.	-43		-1.2	
Mi, et al. - 1965	Holstein	-1 to -133	0	.3 to -4.6	Yes

(4) There are genetic differences in response to inbreeding as shown by variation among sires or lines in inbreeding effects.

(5) The change of performance with inbreeding tends to be directly proportional to the coefficient of inbreeding as shown by lack of non-linearity of inbreeding effects on various quantitative traits.

(6) Inbreeding appears to delay the development of physiological processes in animals as shown by a decrease in difference between inbred and outbred animals with advance of age.

(7) Characters which are subject to inbreeding depression show some heterosis when inbred lines are crossed or inbred animals are crossed to non-inbred unrelated animals.

Unpredictability of inbreeding in stock of different genetic origins, tendency of lower reproductive and productive efficiency, and lack of uniformity in performance of inbred individuals discourage the development of inbred lines as a general means of improving dairy cattle. Development and maintenance of inbred lines would be too costly and crossing of such lines may not produce individuals clearly superior to individuals resulting from outcrossing. Although inbreeding may aid selection by redistribution of genetic variances of additive genes, the application of traits responsive to inbreeding and which show dominance remains obscure.

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Ohio NC-2 Dairy Cattle Breeding Project

Title: Improvement of Dairy Cattle Through Breeding (General and Specific Combining Abilities)

Cooperating Agencies: Dairy Cattle Research Branch, USDA, Ohio Agricultural Experiment Station, and Ohio Department of Mental Hygiene and Correction.

Presented at Symposium - Inbreeding and Line Crossing as Tools in Animal Improvement

Sponsored by USDA. AHRD Genetics Council
April 14-15, 1965

The project in Ohio is an attempt to determine if specific combining abilities could be economically utilized in the Holstein breed. An agreement with the Ohio Department of Welfare and Correction permitting the use of some state-owned herds was arranged for the following reasons: (1) The development of lines prior to crossing was considered necessary because fairly distinct subgroups within the breed were not available and/or research in other species indicates that for maximum performance through crossing, it is important to start with lines or strains which are of high additive genetic merit. (2) Large herds with a permanent ownership were available through the Department without great cost. The agreement states that herd production levels should not be lowered, that the project formulates the mating plans, and that the project is interested in intraherd selection for milk production to the extent this is compatible with the line development maintenance, and the crossing procedures followed.

The limitations imposed on the research project by working with state herds can be inferred from a description of these herds. There are limited numbers of grade cattle in some herds, and in these herds the sire selection program is limited to those cows that are registered. Each herd is enrolled on DHIA or DHIR production testing. Each herd has facilities for handling approximately four mature bulls, however, personnel have been trained to inseminate cows with frozen semen. While the herds are under different managements, the central office in the Department of Welfare and Correction has a state agriculture leader who coordinates all farm efforts and to some extent oversees dairy herd management. The objective of the herds is to provide milk for the institutions. The obligation of the project not to decrease production indicates that the inbreeding incurred in line development should decrease the milk produced only slightly; or, preferably, any decrease due to inbreeding should be obscured by the additive genetic superiority of the cattle or improving environment. There is evidence that each of these two factors have favorably influenced herd performance.

In an attempt to insure adequate numbers to permit both line crossing and line maintenance and also to prevent interbreeding of the lines it was decided, in general, to develop one line at each herd. In 1948 three institution herds milking approximately 100 cows each and one 200-cow herd

were enrolled. Later, three more herds were enrolled. In the 200-cow herd a second line was established. Two of the three herds added later were considerably smaller and these two herds represent one line. At the present then we are working with seven lines. We are intercrossing four lines representing each of the first four herds. Two of the remaining lines have been developed. The herd management or the bulls introduced to establish the seventh line were not satisfactory. Thus, a later attempt was made to start a line and a few more years will be required for development.

Procedures

Prior to the inception of the project in 1948, varying levels of relationship existed among some bulls used in different herds. Therefore, two or more bulls 25% or more related to each other were introduced into each herd, these bulls and their progeny replaced the bulls that were formerly used. The following criteria were employed in selecting the bulls that were used to establish lines: Two or more related bulls were available. Bulls assigned to establish different lines were not related to each other. The bulls were deemed to be of desirable additive genetic merit. A line was defined as a group of animals that have a minimum *inter se* relationship of 20%. A specific first objective of line development was to build the required levels of relationship among a number of animals after 2 or 3 generations. The entire herd,

herds added later were considerably smaller and these two herds represent one line. At the present then we are working with seven lines. We are intercrossing four lines representing each of the first four herds. Two of the remaining lines have been developed. The herd management or the bulls introduced to establish the seventh line were not satisfactory. Thus, a later attempt was made to start a line and a few more years will be required for development.

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which for the duration of the project must act as a reservoir to aid in supplying line animals that would be equivalent from the standpoint of genetic relationship, however, was considered in formulating the mating plans for each herd. All the animals in the herd at any time would not be in the line, and considering the many possible groups in each herd fitting the line specification, the line of our interest is the one from which parents are selected to produce line cross progenies. The general goal of line development, therefore, was to provide a line of related animals and to permit both line crossing and line maintenance to continue for a number of generations. Commensurate with the preceding plan and with defining a line on the basis of *inter se* relationship, effort has been exerted to hold the increasing levels of inbreeding accompanying line development toward a minimum. The primary criterion for selecting bulls for line development and maintenance has been the expected inbreeding of their daughters and their genetic relationship to the line and herd. Some of the selected bulls were required to be line animals in order to produce line cross progenies in addition to maintaining the herd. Up to the present time, from 10 to 18 bulls have been used in line development in each herd. It has seemed desirable to have from 4 to 6 bulls available at all times, as has been the case, to provide some genetic diversity and prevent a rapid accumulation of inbreeding. Currently it is planned to specify

matings from which two or more bulls can be saved each year. Routinely, small quantities of semen have been frozen on most bulls with larger quantities being stored on more important bulls. To the extent that selection for milk production has been compatible with line development, efforts have been made to consider this in sire selection.

Line crossing was started among 4 lines in 4 herds when line development in these herds had progressed to the point at which the line could be maintained with crossing. Frozen semen from the 3 other lines was stored at each of the 4 herds to produce 6 line cross progenies and their reciprocals. Only those line females that had not completed one lactation have been bred to produce line cross progeny to reduce the selection practiced on the dams. Bulls selected to produce line cross progenies were selected, as were all sires, to maintain the line, but in addition these bulls were in the line and at the time did not have daughters in milk. Approximately 30 females have been selected from each line each year and assigned at random to be bred to 2 bulls of each of the other 3 lines. When one of these bulls has 3 or 4 daughters in another line he is replaced in that line by another bull so more bulls can be sampled. Two bulls from each line are sampled simultaneously, but additional bulls are added individually to avoid complete bull and time confounding. It was thought that an analysis of the results attained could be undertaken when there

were 10 to 12 line cross progeny within each cell in each herd.

Production, growth, and body conformation traits are taken on these animals. Production characteristics include milk, fat, solids-not-fat and protein. Concerning growth, body measurements are taken at 5, 12, and 19 mos. of age, 3 mos. after first calving, and 3 mos. after calving beyond 5 yrs. of age. Also heart girth measurements are taken after birth and at 1, 2, 3, and 4 months of age. Dairy type evaluations on a 10-category breakdown basis are taken along with the 7 body measurements.

Current Status

Programs were developed to expand and contract numerator relationship charts and have been applied to one herd. All animals currently in this herd have an average *inter se* numerator relationship of 19% and an average inbreeding of 7%. The animals selected this year to produce line cross progeny have an average *inter se* relationship of 33% and an average inbreeding of 11%. The inbreeding coefficients of the last 50 animals born in this herd, excluding line cross progeny, range from 4 to 18% and average less than 12%. Corresponding values for the other three herds currently being crossed are expected to be similar. An analysis of the effects of inbreeding in these herds indicated the following results: The intrasire regressions of first lactation actual milk and

Production, growth, [illegible]d body conformation traits are taken on these animals: production characteristics include milk, fat, solids-not-fat and protein. Concerning growth, body measurements are taken at 5, 12, and 19 mos. of age, 3 mos. after first calving, and 3 mos. after calving beyond 5 yrs. of age. Also [illegible] girth measurements are taken after birth and at 1, 2, 3, and 4 months of age. Dairy type evaluations on a 10-category, breakdown basis are taken along with the body measurements.

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fat on 1% of inbreeding were -41.3 ± 9.2 lbs. and -1.24 ± 0.33 lbs. respectively. The regressions were similar with larger standard errors for the second lactation; for the third and fourth lactations there were no apparent effects. The intrasire regressions of heart girth on inbreeding were significant at the 5% level of probability from 3 months of age through 3 months after first calving but not significant after 5 yrs. of age. The maximum regression, which occurred at 3 months after first calving, was $-.19 \pm .03$ cm.

In each of the 4 herds in which lines are being crossed there are from 10 to 21 line cross females representing a total of 65 animals. Recently a third bull from each line has been added to sire line cross progeny in the other 3 lines. The oldest crosses are now completing a first lactation. Generally the number of females that was selected to breed to bulls from other lines has increased since line crossing was started. This trend, which has been possible through steady line development, will be continued to increase the numbers of line crosses. It is seen that several more years will be required to accumulate the expected numbers of cross animals.

Plans to utilize the 2 or 3 other lines are not concrete. The 4 lines being crossed do not contain adequate numbers to permit adding additional lines in the present crossing program. Mating females of these lines to bulls of the 4 lines while ignoring the reciprocals would yield added information on all

the lines. Also mating females of each of these lines to 2 or more sets of 2 related bulls from which frozen semen could be attained has been considered.

E. W. Brum
T. M. Ludwick
E. R. Rader
H. C. Hines
D. R. Davis
W. H. Rausch

4-12-65

DR. BRUM: Any questions or comments?

DR. BAYLEY: Do you have a timetable on this effort at all?

DR. BRUM: Not a strict time schedule, no.

DR. BAYLEY: Do you have any idea when you might reach the numbers that you are after for some of this activity?

DR. BRUM: Well, we had thought that there should be ten to 12 line cross progeny in each cell to make 30 to 36 total line cross progeny, assuming you had balance, which you wouldn't have. I would guess ten or 15 years.

DR. BOVARD: Did you say that in order to have this program started with the State institutions you'd say that there would not be any decrease of performance of the cattle in the project?

DR. BRUM: Sort of, yes. I had in the writeup that any decline in performance due to inbreeding should either be slight or preferably it should be obscured by improving the environment or the superior additive gene effects, and I also mentioned I think each of those has taken place.

DR. WARWICK: I believe Dr. Young from Minnesota is here. We'd like to hear about the inbreeding project there in just two or three minutes if you could do that.

DR. YOUNG: Well, when I went to Minnesota about five years ago we did have two lines that were being developed, and these lines at that time had about 75 head in each. Since then we have increased the numbers to about a hundred head in one line and the other line is still about the same size it was.

Actually, I wasn't too enthused about inbreeding at that time. Since then I have become quite a bit more enthused, and this is probably because I haven't really got much inbreeding done yet.

One of the things that did bother me was that certainly having just two lines and crossing these wasn't going to really give us very much information. So what we have done was to turn our two lines into strictly cow lines, which isn't difficult to do, of course, and then we could designate them Cow Line I and Cow Line II.

And we have gone out and selected bulls from artificial breeding that have high general combining ability according to the production of their artificial-sired daughters.

We have selected three of these bulls which we can term S_1, S_2, and S_3.

Now, these two cow lines are being developed in experiment station herds so we don't have this problem that Ohio has, although possibly it doesn't make people too happy when we get lowered production. Nevertheless, ordinarily they will put up with this.

We have taken these three selected bulls, and mated them to about 60 cows in institutional herds, and from those we would expect to get about 20 daughters that would come into production, and that would make usable lactation records.

From those 20 daughters we will select five from which to save bull calves. And these five will be mated back to their own sire to produce sons that are 25 percent or so inbred.

We will then take those sons and ordinarily we hope to get about three sons in each of these lines that we can use. We could designate those S_{11}, S_{12}, and S_{13}, for instance, for this first line of sires, and the same way on across the board.

And then we will make the cross between inbred sons of each of these three bulls and the inbred cows from two cow lines.

This, of course, gives us a total of six different crosses which does at least give us two degrees of freedom for interaction. Dr. Legates says 300 might do the job, so we're less than one percent of the way there according to his estimation anyway, but at least that's better than no degrees of freedom.

And, of course, the analysis as far as I'm concerned at the present time would simply be sire lines, cow lines, sire lines x cow lines, and then within sire line, cow line classes.

Then in addition to this, of course, by having these three sub-sire lines or three sub-lines for each sire line we also can get another interaction term between specific sires within a sire line with the different cow lines.

Actually you can get quite a few more degrees of freedom in that interaction than you do in the other.

However, whether or not you really get a very good test on this is a little debatable, because, of course, your numbers go down.

Now, I must admit I would be a little reluctant on numbers as small as Ohio is using, for instance, because it seems to me it's awfully hard to estimate the general combining ability with those smaller numbers. So what we would hope would be that we would have at least 30 daughters within one of these cow line, sire line crosses.

So essentially that's the type of program we have got at the moment. And I'm not sure that if I was doing this over again that I would go ahead and do the same thing. Because in a sense I think that we might make more progress if we took these cow lines that

we have, possibly split them up and have more cow lines with less animals per line, and try to develop some really highly inbred bulls in those lines. And I mean just bulls. I wouldn't worry much about cows. And then take those highly inbred bulls and cross them out on daughters of different sires that have been used in artificial breeding.

I think that as long as you practice quite a bit of selection on your sires from which you are developing inbred sons that you would probably be able to get some of these bulls placed without too awfully much trouble.

In the long run I think you'd probably get a lot more information doing this than you would doing something like I have outlined here.

But, of course, operationally there is a problem, because you have an awful lot of herds from which you have got to be getting data, and even though this routinely comes in on the DHI program, nevertheless I think most people that work with DHI records would be inclined to say you have got to go out and check a lot of these things out, so that there is an awful lot of work involved in trying to do such a project.

I believe that's all I have to say, and thank you.

THE DEVELOPMENT OF INBRED LINES OF CATTLE AND THEIR USES

J. S. Brinks

Inter-Branch Genetics Conference
April 14 - 15, 1965

There has been considerable interest in the development of inbred lines and their subsequent use in linecrossing and topcrossing experimentation in both the plant and animal fields. Much of this interest has centered around 1) the effects of inbreeding on various traits, 2) the response to selection within these closed lines, and 3) the amount and importance of hybrid vigor associated with linecrossing or topcrossing procedures.

The development of stocks by this mating system also affords basic studies on the genetic mechanisms controlling both quantitative and qualitative traits. Information on the relative importance of additive and nonadditive genetic variation for quantitative traits can be obtained. Many qualitative characters such as genetic abnormalities are frequently uncovered and the mode of inheritance reported through the use of inbred stocks.

Inventory

The development of inbred lines or, more appropriately, closed lines, has received much emphasis in the overall beef cattle breeding research undertaking in the Western region. The procedure followed has been primarily selection for important performance traits accompanied by mild inbreeding. However, the Colorado Station has attempted to inbreed as quickly as possible in the development of their lines.

Currently, there are 39 closed lines in the Western region including 2 Angus, 2 Shorthorn, and 35 Hereford lines. Ten Hereford lines are maintained at the Colorado Station and another 8 at the United States Range Livestock Experiment Station, Miles City, Montana. Other stations that have 2 to 5 lines are Oregon, Wyoming, Montana, New Mexico, Nevada, and Utah.

In the Southern region, information on 6 Brahman-Angus lines and 1 Africander-Angus line has been accumulated at the Jeanerette, Louisiana, station. These lines have been recently discontinued and assigned to other experiments. The Front Royal, Virginia, station is continuing with 3 selection and 4 inbred lines of Herefords, and 2 selection and 4 inbred lines in each of the Angus and Shorthorn breeds.

In the North Central region, 4 lines of Herefords are under study at South Dakota, 1 Hereford and 1 Angus at Iowa, and 2 Shorthorn lines at Kansas.

A recent inventory of the inbred lines at experiment stations throughout the country along with related information on numbers, degree of inbreeding, date closed, foundation stock, etc., is available from the Beef Cattle Research Branch.

Effects of Inbreeding

Colorado recently completed a study on the effects of inbreeding using data on 878 heifer and 830 bull calves from 16 inbred lines, linecrosses, and a control group. Inbreeding of calf and dam averaged 30 percent and 20 percent, respectively. A correlation of 0.59 existed between the two variables. Inbreeding had a detrimental effect on all traits studied. Substantial evidence of a curvilinear response to inbreeding was evident although the nature of the response differed markedly between the two sexes. Inbreeding of dam had a greater effect on weaning weight than inbreeding of calf. The effect of inbreeding of calf and dam on postweaning weights in heifers and cows was not significant. However, the results indicated a fairly substantial effect of inbreeding of calf on yearling traits. The effect of inbreeding appeared to diminish with increasing age up to 3 1/2 years.

The Miles City Station reported on a study involving 2,027 calves by 33 sires in one line during the period 1934 through 1959. The traits studied were weights, gains, and body scores from birth through maturity. Inbreeding was relatively mild and increased from 0.7 percent to 21.6 percent during the period and averaged 16.1 percent. Increased inbreeding had a detrimental effect on all traits studied. The effect of inbreeding reached a peak at 18 months of age in heifers and declined somewhat at mature weights. Final weight off test (12 to 13 months) was affected more by increased inbreeding than weights taken earlier in life in bulls. Increases in inbreeding of dam had a detrimental effect on growth from birth to weaning, presumably through decreased milk production. This effect was completely compensated for at 18 months in heifers and was greatly reduced in bulls at 12 to 13 months. There was a differential response by sex to inbreeding of calf and dam in weanling traits. Inbreeding of calf had a more pronounced effect on females than males, whereas inbreeding of dam had a greater effect on bulls than on heifers.

Oregon also recently completed a study on the effects of inbreeding in four lines covering the period 1951 through 1962. A decline in performance was associated with increased inbreeding of calf and dam. Inbreeding of calf effects were greater on preweaning gain than on postweaning gain. Economy of gain was adversely affected by increased inbreeding of animal.

Wyoming reported on the effects of inbreeding in a closed line of Hereford cattle over a ten-year period. The average inbreeding levels in 1962 were 12 percent for the calves and 8 percent for the dams. The only traits affected significantly by inbreeding of calf were 180-day weaning weight, -1.38 pounds per 1 percent inbreeding, and final weight off test, -2.17 pounds per 1 percent inbreeding. None of the traits was affected significantly by inbreeding of dam.

In a New Mexico study now underway, inbreeding of calf had a positive effect on birth weight in both males and females in two Hereford lines. Inbreeding of dam had a consistently negative effect on weaning grades,

condition, and weaning weight in both sexes and both lines. In general, inbreeding of dam had a greater effect than inbreeding of calf on weaning grade and condition, but a lesser effect on weaning weight. Inbreeding of calf and dam averaged 22 percent and 17 percent in the old line and 17 percent and 12 percent in the outcross line, respectively.

The Front Royal, Virginia, data on Angus and Shorthorn lines indicate inbreeding of calf and dam have a depressing effect on preweaning gain and type scores. Inbreeding of calf and dam averaged about 11 percent and 4 percent for the Angus and 15 percent and 10 percent for the Shorthorns over a 14-year period. The relative importance of inbreeding of calf and dam was not the same in both breeds. Inbreeding of calf was more important in the Angus but less so in the Shorthorn. The heifers' type score was more adversely affected by inbreeding than the bulls', whereas the converse was true for preweaning daily gain. Inbreeding had a slightly larger effect at midsummer than at weaning. This is in agreement with suggestions that there is a gradual recovery from depressing effects of inbreeding in early stages of life.

Nebraska reported that in general calves with higher than average inbreeding levels were below average in performance. The effect of inbreeding of dam was negative for all traits at the Lincoln Station but positive for most traits at Fort Robinson. In general, increased inbreeding led to decreased feed consumption and growth rate.

In summarizing the inbreeding results in beef cattle, it appears evident that increased inbreeding is associated with decreases in growth and live scores or grades. In general, the detrimental effects of inbreeding tend to decrease with increased maturity. However, the magnitude and duration of the inbreeding effect appear to vary widely with breed, line, location, sex, and level of environment. Inbreeding of dam has a detrimental effect on preweaning growth of calves. In many cases, this effect is greater than inbreeding of calf. The effect of inbreeding of dam again appears to vary widely with breed, line, location, sex, and level of environment. Perhaps this should be expected.

Response to Selection

Colorado recently completed a study utilizing data on 785 inbred and 77 control calves from 14 inbred lines and one control group covering the period of 1946 through 1962. The average coefficient of inbreeding was 30 percent in this group. Selection differentials for inbreeding of calf and dam were slightly negative indicating selection against homozygosity. Positive selection pressure was exerted for weaning weight and score in both sexes and for final weight off test, average daily gain, feed efficiency, and final grade among the sires. Considerable positive genetic progress was expected in all traits. Repeat mating and control line information both indicated strong positive environmental trends over years. Estimates of genetic change pooled over all lines were negative for all traits studied except feed efficiency. The level and rate of change of inbreeding appeared to have been real factors in the response of individual inbred lines to selection.

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Response to Selection

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In the Miles City study on one large line over a 25-year period, selection differentials for inbreeding of calf and dam indicated small but consistent selection against homozygosity. Selection pressure for weights, gains, and scores was fairly intense and considerable positive genetic change was expected in all traits studied. Estimates of genetic change from repeat mating information in birth weight, weaning weight, and weaning score were slightly more than expected. Comparisons of expected genetic response and actual phenotypic response for postweaning traits indicate that the response was as great as or greater than expected. Although environment is a factor in these trends, there apparently has been some genetic response and the data do not suggest that this response is less than expected.

In a Havre, Montana, study, 10 years' data on selection intensities and time trends were evaluated in three inbred Hereford lines and their linecrosses resulting from mating to a common tester line. Within-line selection was fairly intense for traits associated with growth. Estimates of genetic progress calculated from repeat mating information were positive for birth and weaning weights and were somewhat larger than expected. Phenotypic time trends were positive for postweaning daily gain of bulls and steers. In general, those lines in which selection was most intense showed the greatest estimated genetic progress.

In the Oregon study, selection intensities were positive for all traits studied and were much greater among males than among females. Automatic selection against inbreeding occurred on the sire side in conjunction with selection for increased performance. In general, performance increased early in the program, then leveled off, and subsequently declined. General improvement in all traits occurred only in the Angus line.

All animals were selected on the basis of final weight in the Wyoming study. Annual selection differentials for birth weight, 180-day weaning weight, postweaning daily gain, and final weight were all positive. The phenotypic regression on years indicate substantial improvement in all traits over a 10-year period.

Other stations in the process of assessing genetic progress within closed lines include Utah, Nevada, New Mexico, Front Royal, Virginia, and Jeanerette, Louisiana.

In all studies reported, there was selection against increased homozygosity as shown by negative selection differentials for inbreeding of calf and dam. This also suggests that the actual degree of homozygosity within these lines may be less than the calculated coefficient of inbreeding would indicate. Response to selection appears to be effective in several lines where inbreeding increased slowly although the separation of the phenotypic trend into the genetic and environmental components is not clear-cut. Where inbreeding increased at a rapid rate in small lines, the general response within the lines appears to be ineffective or negative in direction. However, certain of these lines have shown some

response and several have shown high combining ability when topcrossed to industry cattle. Between-line rather than within-line selection seems to be more effective under this procedure.

Linecrossing and Topcrossing

A preliminary analysis of the data from the Oregon Station dealing with diallel matings among three Hereford lines indicated linecross calves were more economical in feed use than inbred cattle and scored higher. Linecross calves (inbred dams) gained 0.09 of a pound per day faster in the preweaning period and 0.12 of a pound per day faster during the post-weaning period. Linecross calves required 27 pounds less feed per 100 pounds gain than inbred calves.

In the Havre, Montana, study, comparisons of inbred lines with their line-crosses indicate that in general performance for final weight is predictive of relative growth rate at various stages of development in the respective linecrosses. Comparisons between linecrosses and the mean of the parental lines show an average hybrid advantage of 0.1, 4.6, 4.3, and 4.7 percent for birth weight, weaning weight, postweaning daily gain, and final weight, respectively. These crossline steers have exceeded steers from commercial herds of the same breed by 14 percent and 12 percent in feedlot gain in two years where all animals were fed at the Experiment Station.

Preliminary results from the Miles City linecrossing study using five lines indicate that linecross bull calves have a 3 percent advantage in birth weight, 6 percent in 180-day weaning weight, and 3 percent in weaning score over contemporary inbred calves. The linecross bulls gained 3 percent faster in the feedlot and weighed 4 percent more at the end of the test. The linecross heifers weighed 3 percent more at birth, 9 percent more at weaning, scored 3 percent higher at weaning, and weighed 10 percent more at 18 months of age. Again, line performance was indicative of performance in the cross.

The South Dakota study includes the production of inbred, topcross, single cross, and control animals. Controls are under mass selection for some traits but inbreeding is avoided. The comparison of single cross performance with inbred performance is the traditional measure of hybrid vigor. Comparison of control and single cross yields a measure of improvement that might be expected in commercial production using these mating systems. The topcross calves in comparison with the control calves allow an estimate of the value of inbred bulls used on unrelated cattle as opposed to non-inbred bulls so used. The first five years' data indicate that adjusted weaning weights of the topcross, single cross (inbred dams) and control lines are about equal. The inbred calves averaged 17 pounds less than controls. Limited information on postweaning gains and weights indicate the topcross and single cross cattle are superior to the controls. Inbred calves apparently

compensate somewhat for poorer preweaning performance and postweaning weights equal those of controls. While these results are based on few numbers, the comparison of single cross and inbred calves indicate that hybrid vigor is present for growth traits but the use of the inbred cow prevents hybrid vigor from appearing until yearling age.

The Colorado Station reported that linecross female and male calves weighed 15 percent and 8 percent more at weaning than inbred contemporaries, respectively. The majority of the linecross calves were by linecross dams. Inbreeding of calf and dam averaged 33 percent and 24 percent, respectively, in the inbred group. Possible explanations for the differential heterotic response by sex were discussed.

The Arizona Station reported essentially no difference in weaning weight between topcross progeny from nine Hereford sires representing four inbred lines as compared to eight outbred Hereford sires from local sources when all were mated to a common female source. Reporting on the same data on full yearling weights, heifer and bull progeny from inbred sires weighed 6.3 and 12.1 pounds more, respectively, than progeny by outbred sires. However, these differences were not significant.

In summing up, heterosis for growth traits is evident when linecross values are compared to the average of the parental lines. In general, the hybrid advantage for growth appears to be greater in postweaning gain than in preweaning gain when linecross calves are from inbred dams. This is somewhat in contrast to crossbreeding studies where dams were all outbred. Linecross and topcross calves generally excel outbred calves for growth traits. Again, the amount of heterosis appears to vary somewhat with sex and level of environment.

Current and Future Programs

Current programs concerned with line development already mentioned will be continued with the exception of the breed-cross lines at the Jeanerette, Louisiana, station. Short-term linecrossing projects underway at Miles City, Oregon, and Utah will be completed soon. Continued linecrossing will proceed at Colorado, South Dakota, and in the recurrent selection project at Havre, Montana.

The Arizona Station, in cooperation with other stations in the Western region, has initiated a four-year project involving the testing of ten inbred Hereford lines developed at various experiment stations. Ten bulls representing the ten lines will be tested each year for a total of 40 bulls over the four-year period. Information on topcrossing and general combining ability of the lines will be obtained and compared to controls produced by industry bulls on the same cow herd. In addition, semen is being collected, frozen, and used at other locations to assess the importance of genetic-environmental interactions.

A topcrossing program for the Shorthorn lines of the Front Royal, Virginia, experiment is being initiated at the Blacksburg, Virginia, station. About 120 to 140 high grade and purebred Shorthorn cows will be mated to one bull each year from the four inbred and two selection lines. Daughters of these bulls will be mated to bulls of other lines. Information on the use of inbred bulls in topcrossing and linecrossing will be obtained.

The Mississippi Station is initiating a similar study using the Angus lines from the Front Royal station. Sires from the four inbred lines and two selection lines will be used each year.

Work in the area of rotational linecrossing is contemplated at Clay Center, Nebraska. This system would be compared with other selected strains and breed crosses to determine whether the rotational linecrossing program has real potential.

Future Needs

One of the immediate items of importance is to assemble and report information on fertility, survival, and overall reproductive efficiency in inbred, linecross, and control cattle.

Inbred and linecross stocks should be utilized to a greater extent in studying basic problems in fertility to get at the underlying genetic and physiological mechanisms controlling reproduction. These genetically diverse stocks could be utilized in studying the various constituents of body fluids and tissues and their relation to production and quality of product. Information of this type could lead to a better understanding of the basic factors underlying the phenomenon of heterosis.

Information on the use of inbred lines in breed crosses in comparison with outbred crosses should be obtained. The use of specialized sire and dam lines for greater total performance should be explored. Female lines might excel in reproduction, maternal ability, and efficiency of maintenance, whereas sire lines might excel in growth, efficiency to market weight, and quality of product.

Cattle are grown over a very wide range of climatic and nutritional environments. Results to date indicate that more study is needed in the area of microgenetic-environmental interactions. What is the optimum nutritional environment for the greatest expression of heterosis? Are there thresholds of environmental stress where inbreds will not perform adequately?

The use of inbred stocks also affords an efficient method of assessing the importance of macrogenetic-environmental interactions and should be utilized more in this area.

The development of inbred stocks and their subsequent use represents only one area of beef cattle breeding research. Emphasis in this area has to be balanced in relation to the total research effort.

DR. KYLE: You mentioned this briefly. Is there any information to amount to anything on, for example, calving percentage with inbreeding, regression of calving percentage on inbreeding or number of steriles?

DR. BRINKS: I would say very limited information in beef cattle. Some of the other fellows may have more information on this than I do.

But there is some limited information, I think, in the South Dakota study which shows the same general trend as in dairy cattle.

Also data from the Miles City station was classified by various levels of inbreeding, five per cent and ten per cent, and so on. I forget exact amounts but this data showed a decrease in all aspects of fertility and reproduction with increased inbreeding. These were pretty gross classifications, however.

DR. BLACKWELL: You spoke on new top crosses in Arizona about selecting one bull from each of ten different lines.

DR. BRINKS: Right.

DR. BLACKWELL: We have all worried about sire selection in line testing. I can visualize quite a widespread area of genetic diversity within the line yet even though it's called an inbred line.

Are you aiming at the mean of this line or one extreme or the other? Can you comment on this?

DR. BRINKS: No, we are not aiming at the mean. We are trying to pick the best available sires within each line. We think possibly we can maintain the selection differential a little better this way over all lines. At least they will be comparable.

We are doing this by trying to use bulls that have already been used at the home station. If the fellows think enough of them at the home station to use them, we think we are getting top bulls of the line.

DR. BLACKWELL: Do you think this fairly evaluates the line mean and its ability to reproduce this superior top cross ability if you find it?

DR. BRINKS: Not necessarily. However, we are going to use four different bulls per line over a four-year period here. In other words, the same ten lines will be tested all four years but a different bull from each line. In fact, we may continue this and actually use more than four, but it's set up for four years now.

In these very small inbred lines, it seems you get only a small number of very outstanding bulls. Some of them have actually gone into AI studs, and so forth. And it's hard to get a replacement for that herd sire back in the line. There are very few that are nearly as good as him.

DR. ERCANBRACK: Do you use the lines about the same size?

DR. BRINKS: Throughout all these studies?

DR. ERCANBRACK: This particular one of ten.

DR. BRINKS: No, the bulls come from lines of varying sizes. There are two bulls coming from Colorado from lines of only about 20 cows each, two from Nevada with about 30 cows in each of those lines.

DR. ERCANBRACK: This is going to affect your selection in those lines -- just the difference in size.

DR. BRINKS: You bet. Most of them I would say are two-sire lines. I think they all are, even though they only have 20 cows or 30 cows. Some of the lines have up to 60 cows.

DR. KINCAID: You will know what your selection differential is for this particular bull -- that is, where he stands in the line.

DR. BRINKS: Right, in that particular line with those numbers available. That's right.

DR. TEMPLE: In the South Dakota study you indicated weaning weights of the top cross, single cross and control lines are about equal. Are the controls there selected?

DR. BRINKS: As I understand, the controls are selected. I should have Keith talk about this. Keith, do you want to comment on that?

DR. GREGORY: They are selected in the same manner. A much larger line is what we are talking about. In other words, rate of inbreeding is appreciably different.

DR. TEMPLE: Is the selection differential greater in that line than the inbreds?

DR. GREGORY: It would probably be a little bit greater, yes. It would certainly be more stable from year to year, because you're dealing with a larger number so you wouldn't get the fluctuation difference which you get in a small line.

DR. TEMPLE: In line with what was said this morning, isn't that same thing about true with the comparison of controls at Colorado with the line crosses and also with some of the other work in the Western Region?

DR. BRINKS: Yes. In some cases industry cattle have been used as controls. In South Dakota it is a selected line of larger size. In the Colorado work it's industry sires. The line cross cattle in each case have been superior to the outbred cattle.

DR. TEMPLE: Then how do you account for your statement that line cross and top cross calves generally excel outbred calves for growth purposes?

DR. BRINKS: Isn't that what I said?

DR. TEMPLE: It's just the opposite of what you said.

DR. BRINKS: I didn't mean to if I said that. Line crossed calves and top crossed calves, based on the results that we summarized here, generally excel outbred, and when I say "outbred" now I mean industry cattle or control cattle.

DR. TEMPLE: That isn't what you said about the South Dakota one.

DR. BRINKS: Yes, I think it is. That's what I meant to say, Bob. Isn't that right, Keith?

DR. GREGORY: What I heard you say is selected bulls is what you're talking about instead of inbreds. In other words, selected bulls on these industry stocks outperformed the straight industry stocks. Your heifer data. Your South Dakota data.

DR. TEMPLE: What I'm talking about is the line crosses.

DR. GREGORY: Jim didn't have the information on the difference between the lines and crosses. And what you say certainly pertains to the discussion this morning. But the amount of heterosis involved in the different lines is a variation. The average is the same as Wendell put up for his two lines, but it varies with different crosses.

You didn't get all the information, did you, Jim?

DR. BRINKS: I got a fair amount on that. I'm still not sure what Bob's question was, whether he was comparing top cross and line cross or these in combination with industry or just what.

DR. TEMPLE: I'm just trying to nail you to the cross here. (Laughter) And I want to know which cross. (Laughter)

I've got your paper, and you say that the first five years' data -- this is talking about the South Dakota work -- indicate that adjusted weaning weights of the top cross, single cross, and control lines are about equal.

DR. BRINKS: Weaning weights.

DR. TEMPLE: Weaning weights.

DR. BRINKS: Yes.

DR. TEMPLE: Then on the next page you have a statement there that the line cross and top cross calves generally excel outbred calves. And yet on the South Dakota data -- and you said the same for the Colorado data and also for the Arizona data -- they didn't excel.

DR. BRINKS: Well, in the South Dakota data they excelled I think in the post-weaning, not at weaning time. And as I mentioned, the line cross calf on the inbred dam doesn't allow heterosis to show itself until post-weaning. At least this is one interpretation.

I was using a broad brush there and not speaking of just one specific trait.

DR. TYLER: When you were talking about a selection differential a few minutes ago, what particular trait were you thinking about? Is this post-weaning gain or on particular feed lot or what?

DR. BRINKS: In all these studies we calculated selection differentials on all traits.

DR. TYLER: I wondered if you selected on one trait or do you use an index or how do you do it?

DR. BRINKS: It varies with various stations. Colorado uses an index of pre-weaning and post-weaning gain and scoring. Oregon uses an index. Wyoming uses final weight off test. Miles City over a long period of time actually culled quite a few in weaning time. In calculating that index, in retrospect, most of the emphasis proved to have been on final weight off test.

So it varies somewhat with station.

DR. BAYLEY: This line evaluation work. How are you ever going to be able to say that the performance of the lines is better or worse than what would have been obtained by mass selection alone?

DR. BRINKS: This is, of course, a real good question. Actually the lines as we talk about them are kind of a cross between inbred line formation and mass selection. At least in our beef cattle our inbred lines vary for the most part between 20 and 30 per cent inbreeding. Colorado, lines go up to around 40, some a little higher. So we are not talking about as highly inbred lines as in other species.

DR. BAYLEY: Well, when you top cross and use outbreds from industry, you're dealing with populations where the selection goals have been different than yours, and in a good many cases they haven't even used performance records. Isn't that correct?

DR. BRINKS: Right. We are using this not as a control in the sense that would be true of a selected population but as a control where it's been possibly level all the way across.

DR. WILSON: How do these top crosses and line crosses compare with cross breds?

DR. BRINKS: I guess I just draw on my personal observations at Miles City, and Dr. Pahnish can correct me. All cross breds are under irrigated pasture. I'm not so sure this is better than some on the range. But the cross line project cattle are out more on the range. And we also have the (Char lois) breeding in the cross breds. Where we have the charolois we have increased growth. Between the Angus and Hereford crosses we'd have to say they average a little bit better than our line cross calves. Our line cross calves I would say would average better than our straight Hereford and Angus in the cross breeding experiment.

Floyd, would you like to comment on that?

DR. PAHNISH: I think that's about the way it shapes up right now.

DR. TEMPLE: Jim, in line with Dr. Bayley's comment, I think in a small way we have a pretty good estimate of this in the Front Royal, Virginia project where we have the four inbred lines in each of three breeds as compared to selection lines in each of those breeds. It will be a sample. But then we are initiating, as Jim mentioned, these top crossing experiments at both the Blacksburg and the Mississippi stations that will give us an estimate of how well these inbred lines cross on grade cattle or in an outbreeding scheme.

So it's an estimate at that, comparing what you would have gotten if you had selected for these traits.

DR. BRINKS: Do you have any preliminary information on that, Bob?

DR. TEMPLE: No, we're just beginning these where we are top crossing inbred selection lines on the grade cattle. We're just now beginning that at these stations.

DR. WARWICK: Dr. Comstock.

DR. COMSTOCK: I have a question that maybe is answered already but I guess it's fuzzy. You said line cross and top cross generally or in some instances are superior to the controls I take it. I'm not quite sure here. Have the controls been equally selected?

DR. BRINKS: No, except in the South Dakota experiment.

DR. COMSTOCK: Well, I was going to ask: Would there be any reason to expect or do you expect that line crosses or top crosses would be superior to, say, controls?

DR. BRINKS: This is an area where we need some real critical information, as I think was pointed out earlier here.

I think the South Dakota station is set up to obtain this type of data. And preliminary evidence there is that crosses look little bit better than the so-called control under a similar selection scheme.

DR. COMSTOCK: This reminds me of one thing. There isn't really much selection pressure in breeding generally.

DR. BRINKS: Right.

DR. KINCAID: Jim, have you considered the possibility of using frozen semen from particular bulls for your controls?

DR. BRINKS: Yes, we sure have. In fact, we're working on that right now.

DR. KINCAID: It looks to me like the best possibility for this sort of thing.

DR. BRINKS: Yes. At the Miles City station, semen has been collected--I guess it's about ten years old now -- from bulls varying by about half generations. And I'd surely like to see something like this initiated either on a national or regional basis. It would give us a real good measure of genetic control.

DR. TERRILL: On these inbreeding coefficients of 30 or 40 per cent, is this parents or offspring?

DR. BRINKS: In Colorado there is not a whole lot of difference. There's about 40 per cent in the progeny and 32 or something like that in the parents.

DR. TERRILL: In other words, about 8 per cent difference between parents and progeny?

DR. BRINKS: Yes. In a lot of other lines they are not highly inbred. The Miles City lines, most of them, are between 20 and 30 per cent for the progeny and maybe 18 to 20 per cent for the parents.

DR. TERRILL: How many years has it taken to achieve this?

DR. BRINKS: The Line I cattle was started in 1934. It was a six-sire line for several years, and this is only up to about 25 per cent on the average in the progeny.

The other lines were started later but were smaller lines and inbreeding increased faster so they are about comparable in inbreeding with Line I.

DR. HETZER: You mentioned differences in inbreeding and heterosis effects on the sexes. Is that difference in the same direction in all the studies? And also are these differences statistically significant in each case?

DR. BRINKS: Most of these studies haven't been considered in that much detail. I'll comment on it though a little bit.

In the Line I study at Miles City inbreeding of calf had a more detrimental effect on females, and inbreeding of dam had more detrimental effect on bulls. We think decreased milk production probably hurt bulls more than heifers. The two things are confounded because of highly correlated inbreeding of calf and dam. Colorado inbreeding data was very confused. It looked as if inbreeding effects were curvilinear with differences between sexes. There was much more heterosis in females at weaning time.

DR. WARWICK: Thank you, Jim.

There is just one other little piece of data that I might mention, Jim, and perhaps you passed this over because you didn't think it was too significant.

But the Colorado people have expressed some of these results in terms of pounds of calf weaned per cow bred. In those comparisons, just pulling figures off the top of my hat, so to speak, the inbreds have always been lower than either the so-called control or the line crosses.

The line crosses have averaged essentially the same as the so-called control herd when you take all of the line crosses into account.

Now, one or two of the best lines in these crosses have averaged about ten per cent above the control herd, but they have not exceeded the cross breeding herd.

Is that in line with your recollection of the data from there?

DR. BRINKS: Yes.

DR. WARWICK: I assume you passed it over because you didn't think the numbers were sufficient to say anything about. But I do think they are of some interest.

DR. BRINKS: I think so too. The number of cross breds they have is real small.

DR. WARWICK: Yes, they are.

Inbreeding of Sheep

Resume of Past Work

BY: Clair E. Terrill

In the early work on inbreeding of sheep at Dubois, Idaho, two inbred lines were started in 1929. These were Rambouillets. One of these lines was aimed at body conformation or meat type, and the other line at wool production or staple length. After a few years, the one on wool production was discarded, but the other line is still under way.

Early publications on inbreeding in sheep first appeared in the 1930's. Warwick (1930) and Ritzman and Davenport (1931) proposed the use of inbreeding to eliminate hidden undesirable factors and held the idea that the undesirable effects of inbreeding could be prevented by selection of the right kind of foundation stock, followed by rigid culling against undesirable defects. Similar ideas were presented by Nordby (1949). Generally I think they assumed that if it didn't work out they must not have started with the right kind of stock, or adequate selection had not been practiced with inbreeding.

In the mid-30's the idea was held with sheep that we couldn't expect to make much further gain from selection, that probably private breeders had already made most of the gains that could be made with selection in sheep and that we needed a new system of breeding to go on beyond where we were. Of course, this was just about the time when hybrid corn was coming into much increased use, and the idea was prevalent that by forming inbred lines, later to be crossed, that a superior kind of sheep could be developed.

The lines at Dubois were formed in the period from 1938 to 1940. Originally there were 32 lines of Rambouillets. In general these lines were formed by taking a group of ewes and putting them to a ram, preferably one that was outstanding in some characteristic. The better rams that had been used at Dubois in previous years were grouped with ewes which were related to them. Some rams were purchased and at least ten of the original lines were started from rams that were purchased from individual breeders.

Later there were some additional rams purchased, generally to introduce specific genes into lines. The poll gene is probably the best example. When the lines were started practically all Rambouillets were horned. In the years since it has become increasingly evident that the horns were unnecessary and even undesirable. There has been a tendency, which is still going on, to switch from horned sheep to polled sheep.

Many of the original lines of Rambouillets were really just test lines to begin with so that there was some fluctuation in number, but in the 1940's they settled down to about 30 lines and since then three were culled, one in 1948 and two more in 1952, to bring the number to the present 27 lines of Rambouillets.

The ten Columbia lines were started entirely with station stock. When they were started there were practically no sires in the hands of private breeders that didn't come from the U. S. Sheep Experiment Station or didn't trace very closely to stock from there, because the breed was formed at the Station and did not get into the hands of private breeder until the 1920's and 1930's.

In the Targhee breed there were eight original lines, and there were four Corriedale lines. Then, when the Corriedales were discontinued at Dubois, these four Corriedale lines were mated to four Rambouillet rams each from a different Rambouillet line, to make four new lines of Targhees. In the Targhees a further effort was made to obtain diversity of breeding among the lines from the foundation stock. One line was made by Rambouillet times Columbia, one had Border Leicester blood in it, one Australian Merino blood, and the four I already mentioned were made from Rambouillet times Corriedale crosses.

The original eight Targhee lines traced back to the original crosses made to produce the Targhee in 1927, and these are primarily Rambouillet times Lincoln-Rambouillet to obtain three-quarter fine wool, quarter long wool breeding. The later lines had about the same combination of long wool and fine wool blood, but it did come from different sources. A little later three of the Targhee lines were split and the one-half of each of the three were kept to be selected within the line in the regular way, and the other halves were selected by recurrent selection. These six lines are still underway.

In addition there were three small Targhee lines started from outside blood. These were started by purchasing a young ewe with twin lambs, a ram and a ewe. Three of these were started and two are still going. Those were started in the mid-50's. So we now have 27 Rambouillet lines, 10 Columbia lines, and 20 Targhee lines.

Inbreeding has generally resulted in a decline in body weight at birth, weaning and later ages, and in type and condition scores (Glenbockii and Nahimson, 1945; Hazel and Terrill, 1945, 1946a, 1946b; Terrill, et al, 1947, 1948a, 1948b; Brigis, 1950; Morley, 1954; Ragab and Asker, 1954; and Doney, 1957). Dassat and Sartore did not find a significant effect of inbreeding on weights at birth and 30 days but indicated it might have been offset by selection. For each one percent increase in inbreeding birth weights were reduced by 0.03 pound or less; weaning weights by 0.1 pound or less up to 0.3 to 0.4 pounds; yearling weights from less than 0.3 up to 0.6 pounds; and mature weights from 0.6 to 0.7 pounds. Doney (1959) treated inbred lambs with crude pituitary extract and obtained a highly significant initial increase in growth rate as compared with non-inbred lambs.

Declines with inbreeding were also found for fleece weights, both grease and clean, but the change was somewhat less definite and important than for body weight (Hazel and Terrill, 1946b; Terrill et al. 1947, 1948a, 1948b; Morley, 1954; and Doney, 1957). Small or no effects of inbreeding were shown for face covering, staple length, clean wool yield, fiber diameter, crimps per inch,

fiber density or birth coat (Hazel and Terrill, 1945, 1946a, 1946b; Terrill et al. 1947, 1948a, 1948b; Morley, 1954; and Doney, 1957). Results from Dubois show little effect of inbreeding on skin folds (Hazel and Terrill, 1945, 1946a, 1946b; Terrill et al., 1947, 1948a, 1948b) as contrasted with rather definite effects in the Australian Merino (Morley, 1954; Doney, 1957). Of course, the Australian Merino exhibits a much greater degree of skin folds than do the relative smooth Columbia, Targhee and Rambouillet breeds at Dubois.

Inbreeding appears to cause a definite decline in all phrases or reproduction and viability but detailed studies are sparse. Glembockii and Hahimson (1945) found more abortions, fewer lambs born, more stillbirths, and higher mortality from birth to weaning from inbred as compared with outbred matings. Brigis (1950) reported more stillbirths and abortions from closely related as compared with unrelated matings. Morley (1954) found higher mortality and Doney (1957) found lowered fertility from inbred as compared to outbred matings. Doney (1958) reported that inbred ewes take one or two years longer to reach their peak performance in reproduction or fleece production as compared to non-inbreds. In general, the results from Dubois indicate fewer eggs ovulated, fewer fertilizations, more failures from fertilization to parturition, more failures at parturition, greater losses from birth to weaning and also less viability from weaning age on for inbreds as compared to non-inbreds although careful analyses have not been made yet. Dassat (1958) reported a significant decline with inbreeding in fat percentage and milk yield of sheep.

We soon realized immediately after the inbred lines were formed that the opinion that we had already gained all we could from selection was completely false. Thus, an increasing amount of attention was given to selection and particularly ways of making selection more effective and getting more rapid progress in selection were emphasized. Of course, we were impressed by the fact that by paying a lot more attention to selection within these lines we might not be able to sort out how much of whatever gains we might make was due to selection and how much was due to the fact that we did use this system of breeding.

So then control groups were started in the mid-to late-40's, in each of the three breeds. We called these selected non-inbred controls. They actually are inbred a little bit, or become inbred a little bit, because they are closed to outside breeding. About three or four rams per year are used in each control flock in each breed. Close matings are avoided and the number of ewes has varied from about 180 to 200 in each breed.

After these control groups had been going a little while we also realized that we needed some control on selection because time trends are quite unsatisfactory for measuring progress from selectedion. The environmental changes from year to year in the various traits measured are tremendously greater than the expected genetic changes from year to year. Without some way of measuring environmental changes that take place with years it is extremely difficult to tell whether or not gains are made from selection. So we again

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We soon realized immediately after the inbred lines were formed that the opinion that we had already gained all we could from selection was completely false. Thus, an increasing amount of attention was given to selection and particularly ways of making lection more eff tive and getting more rapid progress in selection were emphasized. Of course, we were impressed by the fact that by paying a lot more attention to selection within these lines we mig not be able to sort out how much of whatever gains we might e was due to selection and how much was due to the fact that did use this system of breeding.

So then control groups were started in the mid-to late-40's, ach of the breeds. We called these selected non-inbred t ey actually are inbred a little bit, or become inbred bec use they are closed to outside breeding. About rams per year are used in each control flock in each tings are avoided and the number of ewes has varied 200 in each breed.

oups had been going a little while we some control on selection because the isfactory for measuring progress from selected- ges from year to year in the various er than the expected genetic me way measuring en ron- ars it is extremely difficult selection. So we again

set up control groups which we called stabilized control groups with random selection and random mating. These were initiated in the mid-50's for each of the three breeds which are composed of 100 ewes mated to 20 yearling rams each year in each breed.

In 1953 some variation was introduced in the lines in the way that they were selected. Before that time practically all the lines had been selected for overall merit on a within-line basis. There were some exceptions. In the original lines I think three lines were set aside to be selected for specific traits, one line for staple length, one line for open face, and one line for mutton conformation. But this selection really didn't go much farther than the initial selection. The idea, after the lines were set up, was dropped for a while and then it was reinstituted in 1953. Then some lines were set up for recurrent selection. In two lines of Rambouillets selection was for inbreeding. In other words, we were interested in determing just how rapidly you could inbreed with sheep. In two lines we selected at random. In other lines selection was for different traits. I think Dr. Ercanbrack will tell you more about this.

Up till this time we had been following about the same procedure of selection in all the lines and we thought we might learn more if the procedure was varied so we could tell what would happen if we followed different procedures, or at least get a better idea. However, because of insufficient sheep numbers, we realized we could not do this on a large-enough scale to really settle the issue as to what difference alternative selection procedures would make in the development of inbred lines.

The early lines varied in size from about 20 to 50 ewes and we debated for years whether it was better to have fewer lines of large size or smaller lines and more of them. I think the latter idea more or less won out in that we decided to try to have the maximum number of lines and simply have them large enough so that we could avoid losing them by accident. Actually, I do not think we have lost any lines this way except the small ones that were started with just three animals.

In general we have found that the rate of inbreeding goes up roughly the same regardless of what you do so long as the line is closed and only one sire is used at a time. There is little difference in the inbreeding that is developed in the lines that were selected for inbreeding as compared with those just selected at random. The inbreeding goes up primarily because only one ram is used each year and because the line is closed to outside blood. The rate of inbreeding may be slowed down by using more than one ram per year and if you use as many as three the inbreeding goes up very slowly, just a small part of a percent a year. The inbreeding goes up

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[illegible] The inbreeding goes up

more rapidly if the same ram is used over a number of years. Generally the way to inbreed at the most rapid rate is to select a young ram and use him until he dies and then pick a young son and use him until he dies, and so on. The inbreeding goes up more rapidly with the greater number of years a ram is used because he is mated to more daughters and grand-daughters and then, when he dies, the rate of inbreeding drops down sharply and then builds up again.

The average increase in inbreeding in these lines of sheep has been about 1 percent per year for the dams. The offspring are about 6 to 7 percent more inbred than their parents. Similar increases have been found by Winters et al., 1947; Issawi, 1950; and Ragab et al., 1952. This compares with an average increase of about 0.1 percent, per year, in pure breeding of sheep (Dickinson and Lush, 1933 with Rambouillets, and Carter, 1962, with Hampshires).

The average inbreeding in the three breeds at Dubois for dams are 23 percent in Rambouillets, 22 percent in Targhees, and 24 percent in Columbias, the offspring being 28, 30, and 20, respectively.

The highest inbred line in each group averages 42-1/2 percent in Rambouillets, about 41 percent in Targhees, and 33 percent in Columbias for the dams, and the lambs are 47, 47, and 36, respectively.

I mentioned that it is fairly obvious that reproduction declines with inbreeding, and a fairly rough comparison can be made between the lamb production of the stabilized controls now which is 105 lambs weaned per ewe bred, or 77 pounds of lamb weaned per ewe bred and the inbred lines where it is 76 percent and 52 pounds of lambs weaned, a difference of 29 percent and 25 pounds, which is roughly 1 percent or 1 pound decrease for each percent inbreeding has increased.

The selected control group is actually below the stabilized controls in lamb production, and I think this probably can reasonably be explained by the amount of inbreeding that has probably taken place in the selected control group in the 17 years that it has been under way. The difference there is 8 percent and 3 pounds of lamb weaned per ewe bred.

It was thought before the inbred lines were started that one purpose of developing the lines was to get rid of recessive defects and we were quite surprised that very few of these showed up. And they did not show up right at the start. Some of them are still appearing for the first time in individual lines. This is probably partly because of the slow rate of inbreeding. It is, no doubt, partly because a particular recessive gene in a line is present in only one or two ewes, and it would not show until it happened to be in a ram that was used. The main ones that have shown up are black color, cryptorchidism and defective jaws. Ragab and Asker (1954) found a simple recessive gene for blindness in an inbred line. Doney (1957) mentioned recessive genes for black skin and wool color in inbred lines of Australian Merinos.

Only a few reports have been made of the crossing of inbred lines to produce heterosis in sheep. Carter et al. (1957) found no advantage of inbred sires over outbred sires when crossed on grade ewes. Doney (1961) reported that inbred ewes were more variable in fertility and in body weight than outbred ewes. He further reported that outcrossing restored performance to that of the original population. Ercanbrack et al. (1962) found that top cross lambs from inbred sires were inferior to those from selected control sires and superior to those from sires purchased from breeders in the Rambouillet and Targhee breeds. In the Columbia breed the top cross offspring of inbred sires ranked slightly below those from purchased rams and slightly above those by selected control sires. Drs. Ercanbrack and Blackwell will give you more on results and plans for crossing of the inbred lines at Dubois.

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PRELIMINARY RESULTS OF THE INBRED LINE TESTING PROGRAM AT THE U. S. SHEEP EXPERIMENT STATION, DUBOIS, IDAHO

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(April, 1965)

Current inbreeding research at Dubois is aimed at testing, in line crosses and topcrosses,of inbred lines most of which were initiated during the past 20 to 27 years as described in a paper by Dr. Clair E. Terrill. The current program also includes testing in topcrosses of sires from noninbred control groups developed by mass selection, sires produced by private breeders and sires from randombred control populations. It further includes comparisons of the wool and lamb producing abilities of female line, line-cross, and topcross progeny under mating and management procedures typical in most respects, of the sheep industry. The results to be reported here are those presently available on the weanling and reproductive phases of the testing program, all phases of which will not be complete until about 1970. Initial matings in the current program were made in 1961.

Materials and Methods

Twenty-seven Rambouillet inbred lines of about 24 ewes per line and 20 Targhee and 10 Columbia inbred lines of about 30 ewes per line are included in the tests. The noninbred selected control groups contain 180 ewes per breed, and the randombred (stabilized) control groups contain 100 ewes per breed. Tests are based upon comparisons among the line, line-cross, and topcross progeny of two sires per line per year. Ultimately, a total of 8 sires from each inbred line and control group plus 8 industry-produced sires will have been tested in topcrosses; and 6 sires from each inbred line will have been included in line-cross tests. Sires to be tested are selected at random equally from the upper and lower half of each line or control group, although no sire having poor semen quality is used. Montana State University at Bozeman is cooperating in the topcross testing, which provides the opportunity to test more sires in topcrosses than in line crosses. Eight or nine test ewes (2 or 3 from each breed) are mated to each sire in the topcrosses, and three ewes from each line are being mated to each sire in the line crosses. Reciprocal line-cross matings are being made. Approximately 23% of the total possible Rambouillet crosses, 31% of the Targhee crosses, and 71% of the Columbia crosses will have been sampled at the conclusion of line-cross tests. Because of the necessity of propagating the lines, line crossing has been accomplished only in alternate years, with straight line breeding for replacements occurring in other years.

Selection in most of the lines and the selected control groups has been primarily on the basis of indexes of overall merit. The indexes include information on body weight, face cover, neck folds, body type (mutton conformation), body condition (fatness), wool staple length, grease and clean fleece weight and wool grade where appropriate. Other factors such as horns or scurs, pigmented wool fibers, physical

defects, inappropriately coarse wool, fertility in the rams, lamb production in the ewes, etc., have been considered at independent culling levels. In six lines selection has been based primarily on single traits, namely, body weight, body type, staple length, or clean fleece weight. In two lines selection was based upon rapid inbreeding. In two others selection has been random. In seven lines selection of sires has been recurrent on the basis of their general combining abilities with a noninbred and unrelated test stock. Selection has always been more intense in the selection control groups than in the inbred lines, since usually only about 3 percent of the available sires were bred in the control groups whereas from 6 to 20 percent were used in the lines. This more intense selection was largely the result of much smaller sire to dam ratios in the control groups in addition to generally superior reproductive rates.

The stabilized control groups have been maintained by random mating with the restrictions that only yearling sires were used and insofar as possible at least one randomly selected replacement sire was chosen from the male progeny of each preceding sire. Each sire was mated to only 5 percent of the ewe population (five ewes per sire). Ewes were randomly selected within ages to maintain a normal age distribution. On rare occasions ewes with severe cases of mastitis have been culled from this group.

The selected control groups were initiated with noninbred stock as comparable in genetic origin to that of the inbred lines as possible. The stabilized controls were initiated by choosing at random within sire groups and equally between sire groups about one third of the entire female and one fifth of the entire male selected control progeny for three successive years, after which the groups were closed.

The weanling traits reported herein have all been adjusted for major sources of environmental variation including age of dam, type of birth and rearing, band in which grazed, inbreeding of dam, age at weaning, and time of observation. Corrections also were made for differences in sex and inbreeding of lamb. The figures for all reproductive characteristics are the actually observed values.

The weanling traits were observed at an average age of approximately 120 days, weight being measured to the nearest pound, staple length to the nearest tenth of a centimeter. Scored traits were estimated on a basis of a five point system with plus or minus scores for each point providing 15 scoring units in all. The lower scores indicate superior merit. Side grade of wool is a coded value of U. S. numerical grades (spinning counts) ranging from 1 as 70's to 9 as 48's.

The reproductive characteristics are defined arbitrarily as follows:
viability of ewes to lambing = ewes at lambing/ewes bred,
fertility = ewes lambing/ewes at lambing,
fecundity = lambs born/ewes lambing,
parturient ability = lambs born alive/lambs born,
viability = lambs weaned/lambs born alive, and
net reproductive rate = lambs weaned/ewes bred.

Note that the first five characteristics as just defined are simply factors of the sixth, net reproductive rate. In addition, viability might have been partitioned into components due to mothering ability, fostering ability, and survival ability had the data permitted.

Results

The following results are based on from one-half to nearly all (depending on the breed) of the line data, one-fourth to one-half of the topcross data, and one-third to two-thirds of the line-cross data which ultimately will be available on weanling and reproductive traits. No data on yearling traits or production attributes of female line-cross and topcross progeny have been included. The A tables and B tables contain information on weanling traits and reproductive characteristics, respectively. The averages of line means in each table are unweighted.

Tables 1A through 3B include data on the inbred lines themselves. The weanling data all have been adjusted to a noninbred basis to facilitate comparisons among lines with differing amounts of inbreeding. A column for weaning weight with the adjustment for inbreeding effects removed also has been included. Selection within the inbred lines has always been based on data adjusted to a noninbred basis to avoid discriminating against the more highly inbred individuals. Selection between lines has been minimal, four being culled in the relatively early stages of inbreeding but only two since 1953. Both of the latter were culled because of small size, in one the result of poor reproduction and in the other the result of extensive culling of genes for black wool. Tables 1B through 3B contain the average inbreeding of all lambs born alive plus that of the dams of these lambs, in addition to information on reproductive characteristics. The average inbreeding of all lambs born alive was almost identical to that of all lambs born and all lambs weaned. Neither was there an appreciable difference in the average inbreeding of the dams of these groups.

Lines 22 and 49 in tables 1A and B were maintained by selecting all replacements at random, using randomly selected yearling sires each year whenever available. No sire was used for more than one breeding season in any event. Relative to the average of all lines, these lines are in a less favorable position in the more heritable traits such as face cover, staple length, and neck folds than in the less heritable traits. Reproductive rate is well below average in both lines. Lines 25, 29, 37, and 45 were maintained by inbreeding followed by outcrossing to other line or noninbred sires each four years. These outcross lines are generally somewhat above average in weaning weight, staple length, and overall merit (index). They are outstandingly above average in reproductive rate and consequently in pounds of lamb weaned per ewe. In line 35 selection has been primarily for clean fleece weight. This seems to have had little effect on increasing

weanling staple length or coarsening weanling side grade of wool. This line is below average in net merit. Selection in line 39 has been almost entirely for increased body weight; and this line is well above average in weaning weight, reproductive rate, and pounds of lamb produced. The above average weight seems to be an indirect result of (rather than the cause of) the higher reproductive rate in this line since reproductive rate has nearly always been superior in the line. Improved body type has been the sole object of selection in line 46, and it seems that little has been accomplished here in spite of a superior reproductive rate in this line. In line 51 selection has been chiefly for staple length; and although this line is not the highest in merit for staple length, it is in the top 15 percent. Rapid inbreeding has been the primary objective of selection in lines 47 and 50. These lines seem to be slightly below average in body type, condition, staple length, and face cover and distinctly below average in reproductive rate. Inbreeding is about average in line 47 but well above average for lambs at least in line 50. Lines 20, 27, 53 and 54 have been maintained since 1957 using the recurrent selection system described earlier. Reciprocal recurrent selection was commenced initially in these lines in 1951 but was discontinued because line sizes were steadily declining. The lines are generally below average in reproductive rate although two are above average in net merit.

Tables 2A and B contain information on the Targhee lines. Selection was on the basis of overall merit in all lines except 5T, 14T, 16T, 17T, and 18T. In line 5T selection was for improved body type, apparently with little success. In line 14T selection was based on body weight only, and this line is among the best in this regard. Selection in lines 16T, 17T, and 18T has been recurrent as previously described, initially with topcross progeny from either line except the one being tested being used as the test stock. The initial procedure was discontinued when most test stock contained components of all three lines. These lines were split from lines 4T, 9T, and 15T, respectively, when recurrent selection test matings were initiated in 1950. Some idea as to the relative effectiveness of the system to date may be gained by comparing appropriate pairs of lines. Concurrently, there seems to be little evidence of superiority of the system as practiced at Dubois.

The Columbia inbred line results are included in tables 3A and B. It is apparent that variation among the Columbia lines in almost all respects is much less than that among the Rambouillet and Targhee lines. In spite of the average inbreeding of 24 and 30 percent for dams and lambs, respectively, the lines do not appear to have diverged greatly in weanling characteristics although some striking differences occur in reproductive rate. This may be a reflection of the somewhat more narrow genetic base from which the Columbia lines were formed.

Tables 4A through 6B contain the topcross results of the testing program by line. The test stock used were commercial ewes of Rambouillet, Targhee and Columbia breeding from five different sources, noninbred and unrelated to the sires tested. Approximately three Rambouillet, three Targhee, and two Columbia type ewes were provided each sire. Test ewes ranged in age from three to six years, and ages within breed were stratified as equally as possible across sires. A common, striking and logical characteristic of the weanling topcross data in all three breeds (tables 4A, 5A, and 6A) is the much reduced variation between lines as compared to the inbred line data (tables 1A, 2A, and 3A). This is evident in nearly all traits except face cover and neck folds, against which the test ewes apparently had not been selected so intensively as the inbred lines. Variation in reproductive characteristics seems not to have been so markedly changed, being a little greater in Rambouillet topcross data and approximately the same in Targhee and Columbia topcross data as in the inbred data.

With the possible exception of lines being selected for weaning weight, there seems to be little correlation between topcross and inbred rankings of lines in which selection is for a single trait.

Line-cross results are presented in tables 7A through 9B. Here again one can see a reduction in between-line-of-sire variation much the same as occurred in the topcross data. The regressions toward the breed mean are somewhat larger for the Rambouillets and Targhees than for the Columbias wherein the between-inbred-line variation was much smaller than in the other two breeds. One also can observe the lack of correlation between line-cross and inbred line rankings of lines in which selection is for a single trait.

A matter of considerable interest is the correlation between the merit of the inbred lines themselves and their merit in topcross and line-cross tests. Accordingly, correlations were calculated (tables 10A and B) between the inbred and topcross results, the inbred and line-cross results, and the topcross and line-cross results for each weanling trait and reproductive characteristic. Few of the correlations are above 0.40, most of these occurring between the topcross and line-cross results in weanling traits. There seems to be little evidence here, therefore, that a line's own merit is a reliable index of its topcrossing or general line-crossing abilities although modest correlations did occur between topcrossing and general line-crossing abilities in some traits.

Tables 11A and B permit comparisons of the results obtained within the three major breeding systems used at Dubois. These systems are characterized, respectively, (within each breed) by the development of several small inbred lines with small amounts of mass selection within most lines, the maintenance of a relatively large non-inbred control group with intensive mass selection within this group (selected control),

and the maintenance of a randombred control group using sufficient sires to hold genetic drift and inbreeding to negligible levels (stabilized control).

It is clear that superiority in most weanling characteristics and in the most important reproductive characteristics usually occurs in the selected control groups. However, the Columbia inbred lines generally rank more favorably among the systems within breed than either the Rambouillet or Targhee inbred lines. The relatively poor showing of the Targhee and Columbia stabilized control groups for some reproductive characteristics undoubtedly has been influenced by the preponderance of young dams in these two groups as a result of their more recent origin.

Tables 12A and B contain comparable information on topcross and line-cross results in addition to those from the three systems previously described. Means for the inbred lines are based on much smaller amounts of data than in tables 11A and B, however. It seems that for the Rambouillet and Targhee breeds, at least, line crossing has accomplished on the average little more than to repair some of the deleterious effects of inbreeding. This system has been less effective in most respects than that utilized in the selected control, although it is true that only the average effects of line crossing have been presented and that some individual crosses may be greatly superior in certain traits. In the Columbia breed the average line-cross results are generally slightly superior to the selected control results. Evidence for some small practical amount of heterosis may appear here. The topcross results are not particularly impressive in any breed. These results, of course, are greatly influenced by the average merit of the test stock.

The relative effectiveness of various systems of producing sires with good general combining ability in topcrosses may be examined in tables 13A and B. The stock used for topcrossing was noninbred, unrelated to sires tested, and reasonably typical of the commercial range sheep industry. The sires used in all topcross tests were randomly selected as previously mentioned, with the possible exception of the purchased sires. It usually was left to the discretion of each private breeder to provide sires representative of his flock for testing, and purchased sires generally were obtained from breeders whose professional reputations were above average. It is evident that in the Rambouillet and Targhee breeds the selected control sires again were more often superior to those from other sources for weanling traits. In the Columbia breed the inbred sires were more often superior. It is clear, however, that differences generally are small; hence, significance may be questionable, although the above pattern of superiority has oft been repeated in less comprehensive tests in previous years.

Sires from recurrent selection lines do not seem to possess unusual general combining ability at this relatively early stage in line development using a modified recurrent selection system. Results in table 13B actually may reflect principally random differences among groups of test ewes (mates) assigned to each category of sires, inasmuch as this table deals only with reproductive characteristics and satisfactory semen was required of all sires used in the tests.

Tables 14A1, A2, and B contain coefficients showing the partial regressions of various traits on percent inbreeding of lamb and dam. The units for scored traits in tables 14A1 and A2 are only one-third as large as those in all other A tables, therefore the coefficients as listed must be divided by 3 to be applied to other values for scored traits. It is convenient to think of and use the coefficients in terms of the smaller scoring units, however, since the smaller unit differences can actually be observed when scoring animals. It is clear that the weanling trait most importantly affected is weaning weight (and, consequently,average daily gain). Body type and condition are also moderately affected by inbreeding of lamb. Nearly all estimates indicate that merit declines with increased inbreeding. The most important effects on reproductive traits (table 14B) are the accumulated effects on net reproductive rate and consequently on pounds of lamb weaned per ewe. The estimates for weanling traits were based on individual observations on 500 to 1000 lambs each year, while those for reproductive characteristics were based upon the mean values for each line within breed over the years indicated in table 11B. The biological significance, if any, of the large partial regression coefficients in the bottom of table 14B remains obscure.

In table 15 are listed ratios (in percent) of within sire variances of inbred lines to within sire variances of reasonably comparable noninbred groups of ewes, based on data collected from 1954 to 1959. The degrees of freedom for the variances ranged from 223 to 889 with average inbreeding of the inbred groups as listed at the bottom of the table. There seems to be little evidence, for most traits, that within-line phenotypic variance has been importantly reduced by the small amount of inbreeding which has occurred within the inbred groups. It is possible that the greater intensity of selection that has occurred for most traits in the noninbred groups actually has caused, in some instances, a greater reduction in genetic variance in these than has occurred in the inbred groups. For weanling traits, in particular, a small bias may exist since only those weanling ewes which made yearling records are included in the data. Well over half of the ewes permitted to make yearling records were selected on the basis of a weanling index of overall merit. An alternative possibility is that inbred animals in some respects are more seriously affected by environmental changes than noninbred animals. Thus the small theoretical reduction in genetic variance might have been overshadowed by an increased environmental component in the inbred groups.

Problems

It seems desirable that some of the important problems encountered in the development and testing of inbred lines of sheep should be delineated here for the benefit of those who may be interested.

If many lines are formed, they must be kept small because of space limitations; and, of course, as many lines as possible should be formed and tested. In small lines the potential selection intensity among sires is automatically less than in larger lines, thus genetic progress is inhibited.

The small size of lines creates difficulty in line-cross testing by reducing the size of the sets of lines in reciprocal crosses and thus the rate and sometimes the efficiency (depending upon the number of sets) at which all crosses can be accomplished. Line-cross testing in sheep is also handicapped by the necessity of propagating the lines at least in alternate years.

The test flock required for topcross testing also takes up valuable space, and a compromise between the rate and the accuracy of topcross testing must be reached. Although topcross testing may be somewhat less efficient from the standpoint of genetic information gained than line-cross testing, nevertheless topcrossing at present seems the most probable method through which, genetic improvement of large animals on a large scale will be accomplished. Thus topcross testing with typical commercial stock should be done.

It is extremely difficult to accomplish reciprocal recurrent selection for specific combining ability at a reasonable rate with a species having a net reproductive rate as low as sheep. This form of selection was discontinued at Dubois after 6 years because most resources in the line were being exhausted in testing, with insufficient available for propagation. In range sheep at least half the line must be available for propagation each year to permit replacement of females, with almost no selection. This assumes the net annual reproductive rate at breeding age is about 90 percent. Thus, a line size of 60 ewes would be required for testing 4 to 5 rams annualy at the rate of 6 to 8 ewes per ram, certainly minimal desirable numbers. This would constitute testing only 15 to 19 percent of the potential ram offspring (from 60 ewes) of the line with the standard error of the progeny mean still from 36 to 40 percent of a standard deviation.

Finally, the production of visible lethals or other physical defects does not seem to have been of great consequence in the formation of inbred lines of sheep. Although fertility, fecundity, and parturient ability are each somewhat reduced, the reproductive

factors most importantly affected seem to be viability of lamb from birth to weaning and, as the cumulative consequence of all the foregoing, net reproductive rate. The reduced reproductive rate is a problem, of course, not restricted to sheep; but it is of particular consequence in a species already having a relatively low reproductive rate and long generation interval. The severity of the problem maybe importantly reduced if strenuous management efforts are made to improve viability to weaning of lambs born alive.

Summary of Findings

Selecting within inbred lines for body weight and staple length seems to have resulted in a small measure of success. Selection for body type has been ineffective. Selection for clean fleece weight seems to have had little effect on weanling side grade of wool (make coarser) or staple length (make longer). Lines in which selection has been random seem to be in a relatively less favorable position for highly heritable traits (face cover, neck folds) than for less heritable traits (body type, condition). The lines selected for rapid inbreeding were distinctly below average in net reproductive rate.

One of the major accomplishments of out-crossing inbred lines was to prevent a decline in net reproductive rate.

The correlations between a line's own merit in most traits and its topcrossing and general line-crossing abilities are low. The correlations between topcrossing and general line-crossing ability seem to be moderately high for several weanling traits.

Sheep produced under a breeding system using mass selection and avoiding inbreeding (selected control) were superior in many important weanling and reproductive traits to those produced in inbred lines or in randombred (stabilized control) groups. However, the selected control group is in a relatively less favorable position of superiority (for weanling traits) in the Columbia breed than in the Rambouillet and Targhee breeds.

Although the line-crossing results in the Rambouillet and Targhee breeds appear to be superior in many respects to those in the inbred lines, there is little evidence that line crossing in these breeds has accomplished much more on the average than to repair some of the deleterious effects of inbreeding. The selected control results are generally equally good or superior to those in the line crosses. In the Columbia breed, however, the line-cross results are generally slightly superior to those in the selected control. Evidence of some small <u>practical</u> amount of heterosis may exist here.

The modified system of recurrent selection of sires employed at Dubois does not, at the present stage of line development, seem to possess any unusual merit for improving general combining ability.

A mass selection system of producing noninbred sires for top-crossing on noninbred and unrelated stock seems superior to both the inbred line and recurrent selection systems in the Rambouillet and Targhee breeds. In the Columbias, slightly superior topcross progeny in most traits came from inbred sires.

The only weanling traits in this study (excluding index) importantly affected by differences in inbreeding of lambs were weaning weight (and, consequently, average daily gain) and possibly body type and condition. Weaning weight was also appreciably affected by the dam's inbreeding.

Net reproductive rate and pounds of lamb weaned per ewe bred were the reproductive characteristics most importantly affected by differences in inbreeding, generally through the accumulation of small effects on all components of reproduction.

There is little evidence in the data presented of appreciably reduced phenotypic variation, in most weanling and yearling ewe traits, within inbred lines having approximately 20 percent inbreeding.

It should be emphasized that the above findings were made in most instances without precise knowledge of the probability of error. Many of the findings, however, particularly those pertaining to mating or breeding systems, are in agreement with several years previous results based on less comprehensive data, which lends confidence to their validity.

Table 1A. RAMBOUILLET INBRED LINE ADJUSTED WEANLING AVERAGES BY LINE

Line No.	No. lambs weaned	Weaning weight	Weaning weight less adj. for inbr.	Body type	Body Condi-tion	Staple length	Face cover	Neck folds	Side grade	Index
		(lb.)	(lb.)	(score)	(score)	(cm.)	(score)	(score)	(code)	
19	30	75.0	68.6	2.76	2.68	4.26	3.07	1.26	2.22	142.4
20	23	67.2	62.0	3.24	3.15	4.11	3.36	1.14	2.23	134.5
21	27	77.6	71.3	2.73	2.60	4.60	3.65	1.12	2.10	139.7
22	31	68.9	63.4	3.17	2.86	3.67	3.80	1.82	1.90	116.6
23	40	75.7	71.9	3.09	2.72	3.58	3.89	1.62	1.92	122.5
24	37	77.9	72.9	2.82	2.72	4.12	3.97	1.30	2.21	130.8
25	45	78.7	76.4	2.92	2.58	3.86	3.68	1.22	2.00	134.0
26	25	73.1	67.6	3.20	3.02	3.79	2.92	1.13	2.04	143.7
27	30	73.8	68.1	3.02	3.06	4.08	3.08	1.10	2.06	144.7
29	44	78.0	74.7	2.76	2.56	4.38	2.84	1.08	2.26	150.6
32	34	74.9	70.4	3.24	3.00	3.54	3.39	1.18	1.90	136.0
34	20	72.0	64.8	3.00	2.74	4.04	3.38	1.20	2.19	134.6
35	34	74.0	69.0	3.01	2.85	3.94	3.44	1.46	1.92	132.8
36	21	72.6	67.4	3.04	3.02	4.14	3.29	1.08	2.04	140.6
37	37	74.0	71.1	3.00	2.92	4.26	3.30	1.22	2.10	140.9
39	44	77.8	73.3	3.00	2.70	4.20	3.77	1.40	2.06	133.0
40	20	63.6	54.7	2.93	2.88	3.27	2.75	1.18	1.97	131.6
41	56	77.0	75.8	2.86	2.70	4.18	3.11	1.12	2.08	145.0
44	33	80.1	75.5	2.82	2.65	3.96	2.91	1.25	2.05	147.7
45	41	74.3	71.9	3.12	3.04	4.42	3.20	1.11	2.14	145.6
46	42	69.9	65.1	3.64	3.52	3.74	4.30	1.46	2.05	124.2
47	13	77.4	76.5	3.34	3.02	4.25	3.50	.94	1.94	144.8
49	21	75.4	71.8	3.09	2.78	3.72	3.54	1.34	1.94	132.1
50	15	72.0	70.8	3.36	3.27	4.25	3.57	.99	1.94	139.7
51	30	70.5	65.9	2.79	2.98	4.39	3.26	1.02	2.13	141.1
53	20	69.5	66.6	2.80	2.83	4.54	3.32	1.18	2.14	137.3
54	46	70.7	66.0	2.92	2.90	4.24	2.83	1.09	2.10	145.4
	859									
Ave.	32	73.8	69.4	3.02	2.88	4.06	3.37	1.22	2.06	137.5

TABLE 1B. RAMBOUILLET INBRED LINE REPRODUCTIVE CHARACTERISTICS BY LINE

Line No.	No. ewes bred	Inbreeding Dams	Inbreeding Lambs	Viability of ewes to lambing	Fertility	Fecundity	Parturient ability	Viability	Net reproductive rate	Lbs. lamb weaned per ewe bred
		(%)	(%)	(%)	(%)	(%)	(%)	(%)	(%)	(lbs.)
19	43	34.2	41.7	97.8	81.4	127.1	88.4	78.9	70.4	47.3
20	45	29.9	35.2	97.9	75.3	121.5	74.9	76.8	51.2	31.6
21	43	33.4	38.8	90.8	79.7	131.3	92.9	72.4	62.8	44.0
22	46	32.4	36.6	97.6	80.0	132.5	89.6	73.7	67.7	40.6
23	45	14.8	25.7	100.0	86.0	143.9	95.8	75.3	88.4	62.3
24	45	27.8	32.4	100.0	75.0	137.9	87.7	87.8	81.0	57.1
25	45	8.0	14.1	97.6	83.3	151.7	92.0	87.2	99.1	74.0
26	43	26.4	35.1	100.0	74.5	133.9	89.0	66.1	58.6	38.4
27	42	31.4	36.8	100.0	72.1	140.0	85.6	83.8	71.6	46.5
29	45	13.2	21.3	100.0	88.4	170.7	82.3	78.0	96.7	71.8
32	45	23.4	29.1	97.6	86.2	134.9	85.9	77.5	75.3	53.5
34	31	42.5	47.0	96.7	83.9	143.9	89.2	62.5	64.4	39.0
35	44	25.8	33.9	97.6	79.5	132.4	88.9	85.0	77.2	52.5
36	43	32.9	33.5	90.0	76.9	129.5	78.9	70.8	48.6	33.5
37	45	14.3	18.6	95.2	87.9	136.9	87.6	79.0	81.0	57.7
39	46	20.3	28.9	100.0	91.7	138.2	96.4	79.2	95.6	71.3
40	22	28.6	33.0	95.4	95.2	170.0	91.2	64.5	90.9	51.0
41	46	3.8	7.7	100.0	91.5	166.7	94.2	85.0	121.8	92.4
44	45	25.6	32.1	97.7	79.2	154.9	92.1	66.0	73.3	55.8
45	44	5.1	15.2	97.8	83.6	135.0	93.3	89.1	92.4	66.3
46	45	27.0	31.1	100.0	84.5	133.1	91.8	90.3	92.6	58.4
47	22	23.5	30.6	95.4	71.4	133.3	85.0	76.5	59.1	42.9
49	46	18.6	22.0	100.0	68.2	134.0	82.5	64.0	45.5	33.0
50	23	24.4	38.8	97.8	90.9	115.0	82.6	79.0	65.2	42.6
51	47	25.1	28.8	97.8	62.9	140.4	95.8	77.5	63.8	40.0
53	45	13.7	20.0	95.8	76.6	129.4	85.7	52.9	43.8	29.0
54	46	18.0	30.5	100.0	93.8	163.1	89.7	73.6	100.0	63.1
	1127									
Ave.	42	23.1	29.6	97.7	81.5	140.0	88.5	76.0	75.5	51.7

TABLE 2A. TARGHEE INBRED LINE ADJUSTED WEANLING AVERAGES BY LINE

Line No.	No. lambs weaned	Weaning weight (lb.)	Weaning weight less adj. for inbr. (lb.)	Body type (score)	Body condition (score)	Staple length (cm.)	Face cover (score)	Neck folds (score)	Side grade (code)	Index
1T	36	84.9	76.5	2.51	2.39	4.96	2.98	1.06	2.46	158.2
2T	17	74.0	66.1	2.47	2.21	4.97	2.66	1.08	2.08	150.6
3T	34	78.0	71.7	2.41	2.29	4.75	2.91	.99	2.51	151.0
4T	33	69.7	61.3	2.75	2.76	4.67	3.50	.97	2.15	137.6
5T	14	67.2	61.0	2.71	2.60	4.70	2.80	.99	2.16	144.1
6T	11	78.0	70.2	2.55	2.26	4.77	2.49	1.12	2.29	155.8
7T	35	75.2	67.9	2.64	2.42	4.88	2.68	1.03	2.24	153.1
8T	34	72.6	66.0	2.63	2.54	4.94	3.15	1.01	2.42	145.3
9T	30	79.1	74.3	2.46	2.29	4.88	2.63	1.08	2.35	156.2
10T	42	80.0	76.1	2.60	2.27	4.59	2.65	1.00	2.46	155.5
11T	38	76.5	71.6	2.69	2.66	5.13	2.87	1.00	2.64	155.7
12T	42	78.5	74.1	2.74	2.53	5.04	2.65	1.01	2.51	159.3
13T	34	77.5	71.4	2.55	2.54	5.62	2.86	1.00	3.10	159.4
14T	32	80.0	72.2	2.58	2.42	5.37	2.69	.99	2.91	161.6
15T	31	75.4	70.5	2.69	2.52	4.56	2.72	1.15	2.22	150.0
16T	39	70.0	64.2	2.59	2.47	5.11	3.01	.99	2.84	145.4
17T	24	73.9	70.1	2.74	2.67	4.61	2.81	.98	2.32	150.6
18T	34	71.7	66.9	2.53	2.47	5.09	2.80	1.12	2.86	148.8
20T	14	72.3	62.8	3.18	2.75	4.38	2.12	1.05	2.01	157.9
21T	5	71.7	60.6	2.50	2.92	5.73	2.24	1.03	4.37	166.4
	579									
Ave.	30	75.3	68.8	2.63	2.50	4.94	2.76	1.03	2.54	153.1

TABLE 2B. TARGHEE INBRED LINE REPRODUCTIVE CHARACTERISTICS BY LINE

Line No.	No. ewes bred	Inbreeding Dams	Inbreeding Lambs	Viability of ewes to lambing	Fertility	Fecundity	Parturient ability	Viability	Net reproductive rate	Lbs. lamb weaned per ewe bred
		(%)	(%)	(%)	(%)	(%)	(%)	(%)	(%)	(lb.)
1T	34	32.9	36.5	100.0	91.2	138.7	97.7	85.7	105.9	89.7
2T	30	26.0	35.9	93.3	75.0	138.1	86.2	68.0	56.7	41.8
3T	34	21.4	27.1	100.0	85.3	137.9	100.0	85.0	100.0	82.0
4T	33	27.4	34.9	100.0	84.8	135.7	94.7	91.7	100.0	69.6
5T	17	23.1	27.0	100.0	70.6	133.3	87.5	100.0	82.4	59.0
6T	17	26.8	35.1	100.0	88.2	146.7	90.9	55.0	64.7	52.2
7T	35	25.4	30.9	94.3	97.0	162.5	92.3	72.9	100.0	73.2
8T	32	23.2	29.6	100.0	100.0	134.4	95.4	82.9	106.2	82.4
9T	35	10.9	21.8	94.3	81.8	148.2	87.5	85.7	85.7	72.7
10T	34	11.2	17.2	100.0	100.0	144.1	98.0	87.5	123.5	105.8
11T	32	18.7	21.3	96.9	93.6	151.7	95.4	90.5	118.8	94.2
12T	34	15.7	19.3	97.1	97.0	153.1	95.9	89.4	123.5	100.8
13T	33	15.9	26.4	97.0	84.4	151.8	92.7	89.5	103.0	81.8
14T	34	21.0	33.6	100.0	91.2	138.7	95.4	78.0	94.1	80.2
15T	34	16.0	21.6	94.1	93.8	146.7	90.9	77.5	91.2	73.9
16T	34	20.7	25.3	100.0	97.1	145.4	95.8	84.8	114.7	83.1
17T	34	12.3	17.0	100.0	88.2	136.7	90.2	64.9	70.6	57.6
18T	34	15.7	20.9	97.1	93.9	132.3	97.6	85.0	100.0	78.1
20T	14	31.7	40.4	92.9	92.3	166.7	95.0	73.7	100.0	70.1
21T	7	40.8	47.1	100.0	85.7	150.0	66.7	83.3	71.4	45.9
	591									
Ave.	30	21.8	28.4	97.8	89.6	144.6	92.3	81.6	95.6	74.7

TABLE 3A. COLUMBIA INBRED LINE ADJUSTED WEANLING AVERAGES BY LINE

Line No.	No. lambs weaned	Weaning weight	Weaning wt. less adj. for inbr.	Body type	Body condi- tion	Staple length	Face cover	Neck folds	Side grade	Index
		(lb.)	(lb.)	(score)	(score)	(cm.)	(score)	(score)	(code)	
1	30	76.6	69.8	1.99	2.37	7.51	2.47	1.01	6.19	140.0
2	32	79.3	73.0	2.05	2.20	6.46	2.88	1.09	4.78	138.8
3	30	80.3	73.2	1.99	2.22	6.66	2.47	1.96	5.08	140.1
4	33	81.0	74.5	2.13	2.22	6.10	2.31	1.01	4.29	140.0
5	26	84.1	76.0	2.10	2.39	6.25	2.42	.98	4.65	143.1
6	21	79.4	73.1	2.13	2.21	5.87	2.16	1.14	4.31	135.4
7	36	82.1	76.7	1.97	2.14	7.17	1.72	.99	5.86	142.8
8	32	82.1	77.0	2.00	2.39	6.79	2.34	.97	5.09	143.8
9	28	82.5	74.8	1.95	2.27	6.77	1.78	.99	5.64	140.4
10	35	84.2	77.5	2.01	2.28	6.65	2.48	1.01	5.20	143.6
	303									
Ave.	30	81.2	74.5	2.03	2.27	6.62	2.30	1.02	5.11	140.8

TABLE 3B. COLUMBIA INBRED LINE REPRODUCTIVE CHARACTERISTICS BY LINE

Line No.	No. ewes bred	Inbreeding Dams	Inbreeding Lambs	Viability of ewes to lambing	Fertility	Fecundity	Parturient ability	Viability	Net Repro- ductive rate	Lbs. lamb weaned per ewe bred
		(%)	(%)	(%)	(%)	(%)	(%)	(%)	(%)	(lb.)
1	32	25.3	31.7	96.9	90.3	142.9	95.0	79.0	93.8	71.2
2	34	22.3	29.6	91.2	90.3	142.9	97.5	82.0	94.1	70.7
3	34	27.8	33.1	97.1	90.9	126.7	89.5	88.2	88.2	71.5
4	32	24.2	30.0	96.9	96.8	143.3	95.4	80.5	103.1	79.9
5	32	23.0	29.6	96.9	80.7	152.0	89.5	76.5	81.2	65.7
6	34	22.4	29.0	100.0	79.4	125.9	97.1	63.6	61.8	49.4
7	35	18.6	24.7	100.0	91.4	153.1	85.7	85.7	102.9	80.8
8	35	16.3	23.6	97.1	85.3	141.4	95.1	82.0	91.4	74.0
9	34	33.2	35.7	97.1	84.8	132.1	91.9	82.4	82.4	64.4
10	32	26.4	30.8	90.6	100.0	169.0	89.8	79.6	109.4	83.7
	334									
Ave.	33	24.0	29.8	96.4	89.0	142.9	92.6	80.0	90.8	71.1

TABLE 4A. RAMBOUILLET TOPCROSS ADJUSTED WEANLING AVERAGES BY LINE

Line No.	No. lambs weaned	Weaning weight	Body type	Body condition	Staple length	Face cover	Neck folds	Side grade	Index
		(lb.)	(score)	(score)	(cm.)	(score)	(score)	(code)	
19	16	69.0	2.68	2.72	4.47	3.51	1.16	2.26	132.8
20	15	73.9	2.68	2.86	4.57	3.96	1.19	2.02	132.1
21	22	69.2	2.64	2.88	4.61	4.18	1.38	2.28	122.7
22	16	75.6	2.74	2.68	4.48	3.68	1.36	1.94	134.4
23	19	73.5	2.64	2.74	4.34	4.56	1.56	2.19	116.4
24	8	68.1	2.93	3.09	3.98	3.79	1.36	1.89	124.9
25	14	72.5	2.62	2.80	4.54	3.78	1.16	2.24	133.2
26	22	76.3	2.64	2.80	4.26	3.66	1.44	1.98	133.6
27	18	66.6	2.74	2.92	4.35	3.48	.90	2.34	134.4
29	22	72.0	2.54	2.72	4.81	3.14	1.22	2.64	142.8
32	17	76.8	2.74	2.76	4.46	3.40	1.13	2.14	142.8
34	20	72.6	2.72	2.74	4.56	3.82	1.07	2.30	133.4
35	15	70.8	2.76	2.77	4.53	3.60	1.13	2.16	134.3
36	20	72.8	2.58	2.76	4.60	3.74	1.26	2.39	133.2
37	19	68.8	2.91	2.98	4.38	3.94	1.38	2.08	125.1
39	18	76.8	2.86	2.92	4.38	3.86	1.38	2.22	133.8
40	12	73.8	2.52	2.84	4.38	3.86	1.07	2.39	133.3
41	20	76.0	2.83	2.80	4.60	3.26	1.12	2.40	145.5
44	19	71.3	2.80	2.98	4.38	3.18	1.13	2.23	141.7
45	11	73.4	2.97	2.86	4.46	3.78	.92	2.23	137.0
46	18	74.0	2.64	2.72	4.70	3.69	1.34	2.18	134.7
47	25	73.4	2.66	2.73	4.56	3.66	1.34	2.48	133.6
49	9	68.9	2.84	3.01	4.20	3.90	1.42	1.86	124.6
50	16	77.0	2.76	2.78	4.32	3.34	1.36	2.08	140.5
51	8	70.2	2.43	2.72	4.54	3.44	2.16	2.64	124.2
53	14	70.8	2.52	2.85	5.18	3.34	1.68	2.66	145.4
54	17	71.3	2.60	2.71	4.48	3.79	1.76	2.12	124.2
	450								
Ave.	17	72.4	2.70	2.82	4.49	3.68	1.31	2.23	133.1

TABLE 4B. RAMBOUILLET TOPCROSS REPRODUCTIVE CHARACTERISTICS BY LINE

Line No.	No. ewes bred	Viability of ewes to lambing	Fertility	Fecundity	Parturient ability	Viability	Net reproductive rate	Lbs. lamb weaned per ewe bred
		(%)	(%)	(%)	(%)	(%)	(%)	(lb.)
19	16	93.8	93.3	142.9	100.0	80.0	100.0	77.7
20	16	93.8	100.0	133.3	90.0	83.3	93.8	78.7
21	16	100.0	93.8	153.3	100.0	95.6	137.5	105.2
22	17	94.1	93.8	140.0	81.0	94.1	94.1	75.8
23	16	100.0	87.5	150.0	100.0	90.5	118.8	92.6
24	16	93.8	46.7	171.4	91.7	72.7	50.0	36.9
25	16	100.0	75.0	158.3	94.7	77.8	87.5	68.8
26	16	100.0	93.8	166.7	100.0	88.0	137.5	108.9
27	16	100.0	87.5	150.0	90.5	94.7	112.5	82.4
29	16	100.0	100.0	150.0	95.8	95.6	137.5	107.4
32	16	93.8	93.3	171.4	91.7	77.3	106.2	84.8
34	16	100.0	100.0	156.2	92.0	87.0	125.0	98.2
35	16	100.0	81.2	146.2	94.7	83.3	93.8	71.0
36	16	100.0	93.8	166.7	100.0	80.0	125.0	92.2
37	16	93.8	100.0	153.3	95.6	86.4	118.8	88.2
39	15	100.0	93.3	157.1	95.4	85.7	120.0	101.8
40	15	100.0	53.3	150.0	100.0	100.0	80.0	62.9
41	15	100.0	100.0	146.7	100.0	90.9	133.3	110.3
44	16	93.8	80.0	175.0	100.0	90.5	118.8	86.0
45	16	100.0	43.8	157.1	100.0	100.0	68.8	53.5
46	16	100.0	93.8	140.0	100.0	85.7	112.5	89.8
47	16	100.0	100.0	181.2	96.6	89.3	156.2	117.2
49	15	100.0	60.0	122.2	90.9	90.0	60.0	47.0
50	16	100.0	87.5	150.0	85.7	88.9	100.0	82.9
51	16	100.0	56.2	144.4	100.0	61.5	50.0	36.2
53	16	100.0	81.2	153.8	95.0	73.7	87.5	68.3
54	16	100.0	87.5	135.7	100.0	89.5	106.2	85.5
	429							
Ave.	16	98.4	84.3	152.7	95.6	86.4	104.9	81.9

TABLE 5A. TARGHEE TOPCROSS ADJUSTED WEANLING AVERAGES BY LINE

Line No.	No. lambs weaned	Weaning weight	Body type	Body condi-tion	Staple length	Face cover	Neck folds	Side grade	Index
		(lb.)	(score)	(score)	(cm.)	(score)	(score)	(code)	
1T	41	79.0	2.52	2.40	4.90	2.97	1.18	3.40	150.7
2T	35	78.3	2.60	2.44	4.49	3.16	1.29	2.74	143.8
3T	26	79.5	2.49	2.39	4.76	3.42	1.14	3.59	144.3
4T	29	80.0	2.60	2.50	4.44	3.11	1.34	3.29	145.8
5T	36	77.5	2.40	2.28	5.02	3.19	1.11	3.93	146.7
6T	29	76.2	2.68	2.58	4.95	3.36	1.40	3.62	141.8
7T	26	73.3	2.82	2.71	4.44	2.66	1.14	2.83	149.6
8T	27	78.2	2.62	2.46	4.86	3.17	1.07	3.14	148.6
9T	27	80.4	2.56	2.39	4.74	3.29	1.41	3.40	143.8
10T	33	77.7	2.64	2.48	4.72	3.10	1.15	3.43	147.4
11T	33	80.0	2.61	2.38	4.73	3.34	1.32	3.40	143.4
12T	37	78.1	2.64	2.59	4.82	3.24	1.12	3.64	147.5
13T	38	76.0	2.57	2.56	5.06	3.22	1.37	3.92	144.4
14T	38	81.6	2.54	2.48	4.78	2.90	1.45	3.36	151.5
15T	35	82.5	2.44	2.24	4.78	2.90	1.42	3.14	150.7
16T	35	76.1	2.63	2.48	4.59	3.17	1.30	3.16	142.2
17T	31	80.2	2.67	2.46	4.56	3.14	1.30	2.96	146.5
18T	35	77.2	2.56	2.45	4.80	3.46	1.38	3.44	139.3
20T	37	77.3	2.69	2.54	4.65	2.77	1.18	3.40	151.8
21T	39	78.8	2.62	2.63	5.04	3.18	1.26	3.86	149.6
	667								
Ave.	33	78.4	2.60	2.47	4.76	3.14	1.27	3.38	146.5

TABLE 5B. TARGHEE TOPCROSS REPRODUCTIVE CHARACTERISTICS BY LINE

Line No.	No. ewes bred	Viability of ewes to lambing	Fertility	Fecundity	Parturient ability	Viability	Net reproductive rate	Lbs. lamb weaned per ewe bred
		(%)	(%)	(%)	(%)	(%)	(%)	(lb.)
1T	32	100.0	93.8	158.9	95.0	91.1	128.1	103.9
2T	32	96.9	86.9	153.3	92.9	91.9	109.4	87.2
3T	32	96.9	84.8	142.3	94.3	74.8	81.2	68.5
4T	32	100.0	68.8	162.5	97.6	85.4	90.6	73.3
5T	31	100.0	93.5	159.5	93.1	83.7	116.9	92.4
6T	32	96.9	71.7	168.8	97.6	80.0	90.6	69.6
7T	31	100.0	74.0	142.7	90.8	90.0	83.8	65.2
8T	31	93.8	79.5	146.6	92.3	85.9	86.5	69.7
9T	32	96.9	87.3	136.0	87.7	84.4	84.4	71.5
10T	32	100.0	93.8	141.1	87.5	88.8	103.1	84.2
11T	31	100.0	83.8	148.8	94.7	88.8	105.8	87.8
12T	32	93.8	90.0	158.5	100.0	86.4	115.6	91.1
13T	33	100.0	94.1	142.5	93.3	92.8	115.1	92.0
14T	30	100.0	93.8	150.0	92.1	91.1	118.8	97.5
15T	32	90.6	89.3	156.1	94.9	91.7	109.4	93.0
16T	36	100.0	90.6	152.6	88.7	90.0	109.4	84.4
17T	32	100.0	96.9	141.7	90.0	77.1	96.9	81.3
18T	32	96.9	93.3	156.0	92.4	82.6	109.4	86.9
20T	32	96.9	87.1	148.4	97.5	94.7	115.6	92.4
21T	32	96.9	96.9	166.7	93.8	81.4	121.9	95.2
	639							
Ave.	32	97.8	87.4	151.6	93.3	86.6	104.6	84.4

TABLE 6A. COLUMBIA TOPCROSS ADJUSTED WEANLING AVERAGES BY LINE

Line No.	No. lambs weaned	Weaning weight	Body type	Body condition	Staple length	Face cover	Neck folds	Side grade	Index
		(lb.)	(score)	(score)	(cm.)	(score)	(score)	(code)	
1	30	78.6	2.52	2.54	4.75	3.15	1.30	3.66	130.5
2	35	78.8	2.50	2.45	4.96	3.13	1.18	3.76	132.0
3	32	78.5	2.48	2.53	5.10	3.04	1.24	3.75	133.0
4	34	80.7	2.59	2.44	4.44	3.52	1.33	3.08	132.5
5	23	79.5	2.53	2.44	4.91	3.30	1.18	3.74	132.5
6	27	74.8	2.45	2.36	4.84	3.31	1.21	3.75	126.1
7	39	81.4	2.40	2.33	5.21	3.06	1.12	4.32	133.3
8	30	78.6	2.52	2.32	4.74	3.09	1.65	3.06	132.8
9	25	78.5	2.50	2.50	4.92	3.22	1.12	3.89	130.8
10	28	79.2	2.50	2.42	4.86	3.40	1.28	3.59	132.2
	303								
Ave.	30	78.9	2.50	2.43	4.87	3.22	1.26	3.66	131.6

TABLE 6B. COLUMBIA TOPCROSS REPRODUCTIVE CHARACTERISTICS BY LINE

Line No.	No. ewes bred	Viability of ewes to lambing	Fertility	Fecundity	Parturient ability	Viability	Net reproductive rate	Lbs. lamb weaned per ewe bred
		(%)	(%)	(%)	(%)	(%)	(%)	(Lb.)
1	32	100.0	75.0	147.1	96.2	85.1	93.8	74.3
2	32	96.9	96.9	143.3	95.0	85.1	109.4	90.9
3	32	96.9	84.4	146.1	95.5	89.4	100.0	82.2
4	32	100.0	96.9	141.7	97.5	79.6	106.2	88.9
5	31	96.9	80.0	128.6	86.7	88.7	74.2	65.1
6	32	96.9	71.7	143.8	93.1	90.0	84.4	65.1
7	32	100.0	90.6	144.3	100.0	93.8	121.9	104.0
8	32	100.0	81.2	145.8	92.9	85.6	93.8	78.2
9	31	93.8	72.9	137.5	92.9	92.3	80.2	67.3
10	32	100.0	93.8	140.2	83.6	79.9	87.5	75.1
	318							
Ave.	32	98.1	84.3	141.8	93.3	87.0	95.1	79.1

TABLE 7A. RAMBOUILLET LINE-CROSS ADJUSTED WEANLING AVERAGES BY LINE OF SIRE

Line No.	No. lambs weaned	Weaning weight	Body type	Body condi-tion	Staple length	Face cover	Neck folds	Side grade	Index
		(lb.)	(score)	(score)	(cm.)	(score)	(score)	(code)	
19	19	71.9	2.82	2.79	4.48	3.28	1.07	1.93	140.7
20	22	75.0	2.90	2.76	4.78	3.25	1.00	2.08	147.0
21	13	72.0	2.82	2.80	4.75	3.32	.84	2.15	144.5
22	15	75.9	2.96	2.80	4.28	3.12	1.06	2.02	146.0
23	15	71.6	2.83	2.74	4.54	3.84	1.00	2.10	133.0
24	8	77.0	2.79	2.73	4.83	3.23	1.39	2.08	145.0
25	10	75.8	2.94	2.84	4.28	3.40	1.20	1.64	140.3
26	13	69.8	2.94	3.08	4.36	2.96	1.32	2.04	142.1
27	17	76.6	2.74	2.78	4.71	3.30	1.07	2.06	146.6
29	19	75.4	2.66	2.53	4.64	3.14	1.14	2.00	144.7
32	20	76.0	2.87	2.87	4.70	3.44	.88	2.04	146.6
34	12	66.8	2.98	3.15	4.35	3.78	.87	1.91	132.2
35	21	74.6	2.88	2.82	4.64	3.68	1.08	1.96	138.8
36	20	74.5	3.00	2.81	4.55	3.15	1.10	1.92	145.7
37	21	73.1	2.86	2.87	4.54	3.10	1.02	2.03	146.3
39	20	76.5	3.11	2.90	4.56	3.33	.96	1.94	147.3
40	7	73.8	2.92	2.89	4.34	2.71	.88	1.90	153.3
41	22	77.1	2.78	2.84	4.76	2.80	1.13	2.03	154.8
44	19	76.8	2.94	2.96	4.69	2.84	.90	2.08	157.1
45	7	79.2	2.88	2.88	4.65	3.11	.93	1.94	154.0
46	22	73.3	2.88	2.80	4.36	3.34	1.04	2.02	140.9
47	15	75.8	2.84	2.72	4.66	3.59	1.24	2.03	138.8
49	11	69.1	2.88	2.76	4.58	3.86	.80	1.54	132.8
50	6	74.1	3.02	2.81	4.19	2.92	1.06	1.98	146.8
51	13	72.9	2.86	2.72	4.60	3.73	1.52	2.06	130.3
53	18	68.4	2.80	2.95	4.79	3.24	.99	2.02	141.9
54	22	73.2	2.77	2.78	4.67	2.90	1.14	2.17	148.3
	427								
Ave.	16	73.9	2.88	2.83	4.57	3.27	1.06	1.99	143.9

TABLE 7B. RAMBOUILLET LINE-CROSS REPRODUCTIVE CHARACTERISTICS BY LINE OF SIRE

Line No.	No. ewes bred	Dam's Inbr.	Viability of ewes to lambing	Fertility	Fecundity	Parturient ability	Viability	Net reproductive rate	Lbs. lamb weaned per ewe bred
		(%)	(%)	(%)	(%)	(%)	(%)	(%)	(lb)
19	18	22.1	94.4	94.1	143.8	100.0	82.6	105.6	78.9
20	11	27.6	100.0	94.1	156.2	96.0	91.7	129.4	96.1
21	11	33.5	100.0	90.9	140.0	100.0	92.9	118.2	84.9
22	18	24.8	88.9	93.8	146.7	95.4	71.4	83.3	66.3
23	18	16.8	100.0	100.0	133.3	83.3	75.0	83.3	60.7
24	17	28.3	88.2	40.0	150.0	88.9	100.0	47.1	34.8
25	18	30.8	100.0	61.1	127.3	92.9	76.9	55.6	40.6
26	18	28.7	100.0	72.2	130.8	100.0	76.5	72.2	52.1
27	18	23.0	100.0	83.3	140.0	95.2	85.0	94.4	75.7
29	18	17.3	88.9	93.8	140.0	100.0	90.5	105.6	84.5
32	18	13.9	100.0	94.4	152.9	100.0	76.9	111.1	82.0
34	12	28.9	91.7	100.0	136.4	93.3	85.7	100.0	69.8
35	18	27.0	100.0	88.9	162.5	88.5	91.3	116.7	83.0
36	18	14.7	100.0	100.0	122.2	100.0	90.9	111.1	90.0
37	17	15.8	100.0	100.0	158.8	96.3	80.8	123.5	93.7
39	17	18.9	100.0	94.1	137.5	95.4	95.2	117.6	93.4
40	18	28.0	94.4	47.1	137.5	90.9	70.0	38.9	28.3
41	18	19.3	100.0	94.4	141.2	100.0	91.7	122.2	96.7
44	18	12.0	100.0	100.0	138.9	96.0	79.2	105.6	85.6
45	17	23.9	94.1	43.8	142.9	90.0	77.8	41.2	33.6
46	18	24.5	100.0	100.0	144.4	88.5	95.6	122.2	87.9
47	17	27.8	94.1	87.5	128.6	100.0	83.3	88.2	68.7
49	17	19.4	88.2	46.7	157.1	100.0	100.0	64.7	44.8
50	18	37.9	100.0	60.0	133.3	87.5	85.7	60.0	44.2
51	18	27.2	94.4	76.5	138.5	100.0	72.2	72.2	52.9
53	18	17.1	94.4	82.4	142.9	95.0	94.7	100.0	71.9
54	18	14.6	100.0	94.4	152.9	100.0	84.6	122.2	92.6
	458								
Ave.	17	23.1	96.7	82.7	142.1	95.3	85.1	93.0	70.1

TABLE 8A. TARGHEE LINE-CROSS ADJUSTED WEANLING AVERAGES BY LINE OF SIRE

Line No.	No. lambs weaned	Weaning weight	Body type	Body condi- tion	Staple length	Face cover	Neck folds	Side grade	Index
		(lb.)	(score)	(score)	(cm.)	(score)	(score)	(code)	
1T	60	84.3	2.40	2.20	5.04	2.80	1.19	3.58	158.1
2T	17	76.2	2.57	2.39	4.76	2.80	1.17	2.96	149.8
3T	62	84.0	2.40	2.18	5.05	2.95	1.24	3.60	155.0
4T	35	84.7	2.40	2.32	4.88	3.00	1.36	3.38	153.4
5T	24	78.6	2.40	2.23	4.98	3.09	1.20	3.13	147.7
6T	17	83.7	2.40	2.34	5.34	3.10	1.34	4.08	154.6
7T	48	80.9	2.44	2.39	5.00	2.64	1.18	3.18	158.4
8T	52	82.2	2.45	2.34	5.25	3.09	1.16	3.92	154.5
9T	38	80.4	2.42	2.24	5.02	2.85	1.21	3.12	153.4
10T	44	82.8	2.50	2.31	4.96	2.88	1.27	3.24	154.7
11T	52	81.4	2.47	2.46	5.08	2.98	1.25	3.65	154.1
12T	36	81.0	2.56	2.37	5.15	2.86	1.14	3.27	156.7
13T	59	80.2	2.38	2.36	5.24	2.94	1.20	3.70	154.6
14T	47	80.6	2.48	2.35	5.22	2.77	1.26	3.46	156.4
15T	51	82.2	2.46	2.28	4.96	2.70	1.26	3.34	156.9
16T	48	83.7	2.44	2.24	5.04	3.10	1.34	3.35	151.6
17T	59	86.3	2.48	2.24	4.77	2.78	1.18	2.96	159.2
18T	59	79.5	2.42	2.29	5.19	3.04	1.26	3.54	150.8
	808								
Ave.	45	81.8	2.45	2.31	5.05	2.91	1.23	3.41	154.4

TABLE 8B. TARGHEE LINE-CROSS REPRODUCTIVE CHARACTERISTICS BY LINE OF SIRE

Line No.	No. ewes bred	Dam's inbr.	Viability of ewes to lambing	Fertility	Fecundity	Parturient ability	Viability	Net reproductive rate	Lbs. lamb weaned per ewe bred
		(%)	(%)	(%)	(%)	(%)	(%)	(%)	(Lb.)
1T	52	16.4	92.6	93.5	164.0	97.3	84.6	115.8	96.7
2T	22	24.9	93.8	67.9	157.8	71.4	100.0	71.4	51.7
3T	52	19.3	100.0	86.9	164.5	94.6	88.9	119.9	98.6
4T	48	17.2	97.9	68.6	139.6	91.7	87.3	72.9	62.5
5T	27	26.4	92.6	83.7	155.6	87.5	85.7	89.3	69.5
6T	27	24.6	100.0	58.8	148.3	92.3	80.5	62.6	49.7
7T	50	17.1	92.0	71.0	158.9	96.0	97.5	95.4	79.1
8T	47	18.3	95.8	86.9	161.9	90.8	91.3	110.7	91.6
9T	50	20.7	94.1	85.3	148.0	89.4	70.3	76.9	61.5
10T	48	21.3	97.9	85.0	146.7	83.1	89.4	91.7	74.8
11T	48	19.4	95.8	87.1	150.0	91.1	94.7	108.3	87.2
12T	48	20.1	97.9	64.0	148.6	93.5	87.1	75.0	61.0
13T	52	20.6	100.0	92.6	142.3	95.3	90.3	115.5	92.4
14T	50	18.2	97.9	84.1	155.7	90.1	82.6	94.4	78.1
15T	52	20.6	100.0	88.4	155.0	87.6	82.2	99.1	81.7
16T	50	18.3	93.8	79.0	156.9	97.5	83.3	95.0	77.8
17T	52	21.5	97.9	92.1	144.5	95.0	91.0	112.8	97.7
18T	50	19.5	98.1	91.8	171.3	96.2	80.0	117.8	94.0
	855								
Ave.	48	20.2	96.6	81.5	153.9	91.1	87.0	95.8	78.1

TABLE 9A. COLUMBIA LINE-CROSS ADJUSTED WEANLING AVERAGES BY LINE OF SIRE

Line No.	No. lambs weaned	Weaning weight	Body type	Body Condition	Staple length	Face cover	Neck folds	Side grade	Index
		(lb.)	(score)	(score)	(cm.)	(score)	(score)	(code)	
1	35	85.6	2.12	2.08	5.64	2.33	1.24	5.03	135.9
2	49	89.0	2.00	1.92	5.90	2.58	1.08	5.16	139.9
3	66	86.8	2.09	2.08	5.80	2.39	1.08	5.24	137.3
4	40	86.3	2.11	1.94	5.35	2.56	1.14	4.50	135.8
5	55	85.9	2.00	1.98	5.80	2.50	1.09	5.18	136.0
6	48	84.2	2.08	1.89	5.64	2.60	1.10	4.89	134.4
7	53	87.2	1.95	1.91	6.16	2.38	1.10	5.72	137.6
8	45	86.8	2.02	1.84	5.72	2.34	1.05	5.24	135.6
9	53	85.5	2.08	2.06	5.55	2.50	1.04	5.06	134.4
10	53	82.5	2.12	2.06	5.90	2.67	1.00	5.33	133.8
	497								
Ave.	50	86.0	2.06	1.98	5.75	2.48	1.09	5.14	136.1

TABLE 9B. COLUMBIA LINE-CROSS REPRODUCTIVE CHARACTERISTICS BY LINE OF SIRE

Line No.	No. ewes bred	Dam's Inbr.	Viability of ewes to lambing	Fertility	Fecundity	Parturient ability	Viability	Net reproductive rate	Lbs. lamb weaned per ewe bred
		(%)	(%)	(%)	(%)	(%)	(%)	(%)	(lb.)
1	52	27.4	92.6	79.0	137.3	81.8	83.0	68.4	57.1
2	51	28.2	96.1	87.5	147.7	93.9	83.0	96.8	82.3
3	52	26.8	100.0	88.1	167.7	95.0	90.2	126.5	105.8
4	52	20.1	96.4	71.6	151.9	87.1	81.7	75.6	65.6
5	52	20.4	95.8	77.4	167.0	91.0	92.5	104.8	90.1
6	52	20.5	98.2	85.6	151.9	87.0	82.4	91.4	79.4
7	52	21.5	97.9	84.2	150.3	95.5	86.9	102.4	89.9
8	52	22.0	97.9	74.3	164.3	93.2	75.9	86.0	72.1
9	53	25.5	96.2	86.0	160.8	91.6	82.6	100.0	83.9
10	52	27.2	95.8	86.8	146.5	93.8	86.7	100.3	84.1
	520								
Ave.	52	24.0	96.7	82.0	154.6	91.0	84.5	95.2	81.0

TABLE 10A. CORRELATIONS AMONG THE LINE MEANS OF INBRED, TOPCROSS AND LINE-CROSS PROGENY OF INBRED SIRES BY WEANLING TRAIT

Trait	Breed	Inbred x Topcross	Inbred x Line-cross	Topcross x Line-cross
Weaning Weight (Less adjustment for inbreeding)	Rambouillet	-.05	.34	.17
	Targhee	.24	.19	.18
	Columbia	.40	-.19	.34
	Average	.06	.26	.19
Body Type	Rambouillet	.14	.35	.18
	Targhee	.15	.20	.25
	Columbia	.38	.09	.46
	Average	.15	.31	.21
Condition	Rambouillet	-.21	.02	.11
	Targhee	-.10	.13	.46
	Columbia	.15	.14	.85
	Average	-.15	.05	.28
Staple Length	Rambouillet	.39	.44	.14
	Targhee	.30	.53	.67
	Columbia	.32	.36	.83
	Average	.34	.43	.43
Face Cover	Rambouillet	.42	.48	.37
	Targhee	.01	.35	.70
	Columbia	.05	.22	.72
	Average	.30	.42	.44
Neck Folds	Rambouillet	-.01	-.22	.47
	Targhee	.41	.05	.50
	Columbia	-.25	.10	-.02
	Average	.01	-.19	.43
Side Grade	Rambouillet	.27	.22	.14
	Targhee	.38	.38	.40
	Columbia	.45	.55	.63
	Average	.36	.41	.41
Index	Rambouillet	.32	.33	.49
	Targhee	.21	.47	.58
	Columbia	.79	-.08	.41
	Average	.31	.34	.50

Note: Twenty-seven Rambouillet, 18 Targhee and 10 Columbia line means are involved in the correlations. Correlation required for significance at the 5% level is 0.367 for Rambouillets, 0.444 for Targhees, 0.576 for Columbias and 0.262 for the combined average.

TABLE 10B. CORRELATIONS AMONG THE LINE MEANS OF INBRED, TOPCROSS AND LINE-CROSS MATINGS OF INBRED SIRES BY REPRODUCTIVE CHARACTERISTIC

Trait	Breed	Inbred x Topcross	Inbred x Line-cross	Topcross x Line-cross
Fertility	Rambouillet	.23	.15	.84
	Targhee	-.05	.07	.64
	Columbia	.76	.02	-.04
	Average	.21	.12	.76
Fecundity	Rambouillet	.01	-.10	-.48
	Targhee	-.24	-.31	.06
	Columbia	-.31	-.33	-.40
	Average	-.06	-.18	-.33
Parturient Ability	Rambouillet	.43	-.23	.15
	Targhee	.13	.50	.11
	Columbia	.11	-.53	-.13
	Average	.32	-.02	.09
Viability	Rambouillet	-.03	.07	-.11
	Targhee	.18	-.11	.21
	Columbia	.04	.15	.25
	Average	.04	.01	-.02
Net Reproductive Rate	Rambouillet	.10	.03	.56
	Targhee	.16	.34	.13
	Columbia	.55	-.12	-.03
	Average	.15	.10	.44
Viability of Ewes to Lambing	Rambouillet	-.01	-.13	.06
	Targhee	.38	.18	-.34
	Columbia	-.05	.33	-.18
	Average	.08	.00	-.03
Lbs. Lamb Weaned per Ewe Bred	Rambouillet	.19	.10	.59
	Targhee	.23	.39	.17
	Columbia	.58	-.04	.09
	Average	.22	.17	.47

Note: Twenty-seven Rambouillet, 18 Targhee and 10 Columbia line means are involved in the correlations. Correlation required for significance at the 5% level is 0.367 for Rambouillets, 0.444 for Targhees, 0.576 for Columbias and 0.262 for the combined average.

TABLE 11A. MEANS OF ADJUSTED WEANLING TRAITS BY BREEDING SYSTEM

Breeding systems	Year	No. lambs weaned	Weaning weight (lb)	Body type (score)	Condition (score)	Staple length (cm.)	Face cover (score)	Neck folds (score)	Side grade (code)	Index
Rambouillet	1962+1964									
Inbred Lines		859	73.8 (69.4)*	3.02	2.88	4.06	3.37	1.22	2.06	137.5 (133.5)*
Selected Control		325	74.1	2.88	2.78	4.19	2.90	1.18	2.17	145.4
Stabilized Control		203	72.0	2.90	2.72	4.10	3.58	1.26	2.12	131.2
Targhee	1963									
Inbred Lines		579	75.3 (68.8)*	2.63	2.50	4.94	2.76	1.03	2.54	153.1 (147.4)*
Selected Control		223	78.2	2.57	2.58	5.17	2.86	1.02	2.91	156.9
Stabilized Control		93	76.5	2.59	2.59	5.08	2.85	1.09	2.89	154.0
Columbia	1963									
Inbred lines		303	81.2 (74.5)*	2.03	2.27	6.62	2.30	1.02	5.11	140.8 (130.6)*
Selected Control		185	79.1	2.15	2.43	5.95	3.11	1.03	4.80	134.7
Stabilized Control		80	75.0	2.18	2.51	6.01	2.89	.99	4.88	131.2

* Mean with adjustment for inbreeding effects removed

TABLE 11B. MEANS OF REPRODUCTIVE CHARACTERISTICS BY BREEDING SYSTEM

Breeding systems	Year	No. ewes bred	Viability of ewes to lambing (%)	Fertility (%)	Fecundity (%)	Parturient ability (%)	Viability (%)	Net reproductive rate (%)	Lbs. lamb weaned per ewe bred (lb.)
Rambouillet	1962 + 1964								
Inbred Lines		1127	97.7	81.5	140.0	88.5	76.1	75.5	51.7
Selected Control		371	98.9	78.8	139.4	90.7	89.7	87.6	71.1
Stabilized Control		199	99.5	83.8	150.7	94.1	86.7	103.1	66.5
Targhee	1963								
Inbred Lines		591	97.8	89.6	144.6	92.3	81.6	95.6	74.7
Selected Control		185	97.3	92.2	160.8	94.4	88.5	120.5	102.0
Stabilized Control		85	98.8	92.9	148.7	93.1	86.1	109.4	94.9
Columbia	1963								
Inbred Lines		334	96.4	89.0	142.9	92.6	80.0	90.8	71.1
Selected Control		181	97.2	92.6	145.1	94.0	83.7	102.8	90.2
Stabilized Control		100	95.9	77.7	139.7	93.1	84.2	81.6	69.5

TABLE 12A. MEANS OF ADJUSTED WEANLING TRAITS BY SYSTEM OF MATING

Mating system	Year	No. lambs weaned	Weaning weight (lb.)	Body type (score)	Body condition (score)	Staple length (cm.)	Face cover (score)	Neck folds (sc.)	Side grade (code)	Index
Rambouillet- 1963										
Inbred lines		135	74.5(69.0)*	2.89	2.88	4.73	3.18	1.05	2.05	147.4(137.3)*
Line-cross		427	73.9	2.88	2.83	4.57	3.27	1.06	1.99	143.9
Topcross		450	72.4	2.70	2.82	4.49	3.68	1.31	2.23	133.1
Selected Control		203	69.7	2.90	2.94	4.60	2.80	.87	2.08	150.0
Stabilized Control		101	69.4	2.83	2.85	4.58	3.46	1.08	2.03	136.0
Targhee-1962+1964										
Inbred Lines		126	82.4(75.9)*	2.34	2.26	4.87	3.34	1.28	3.15	146.3(137.3)*
Line-cross		808	81.8	2.45	2.31	5.05	2.91	1.23	3.41	154.4
Topcross		591	78.4	2.59	2.46	4.75	3.16	1.27	3.36	146.0
Selected Control		393	82.7	2.72	2.55	4.74	2.78	1.16	3.14	157.9
Stabilized Control		197	77.2	2.64	2.52	4.81	3.08	1.22	3.14	147.6
Columbia-1962+1964										
Inbred Lines		109	76.9(78.3)*	2.16	2.27	5.93	2.18	1.15	5.68	128.1(130.0)*
Line-cross		497	86.0	2.06	1.98	5.75	2.48	1.09	5.14	136.1
Topcross		303	78.9	2.50	2.43	4.87	3.22	1.26	3.66	131.6
Selected Control		311	85.7	2.18	2.28	5.67	2.74	1.20	5.22	136.3
Stabilized Control		158	81.4	2.22	2.32	5.62	2.63	1.06	5.20	131.8

* Mean with adjustment for inbreeding effects removed.

TABLE 12B. MEANS OF REPRODUCTIVE CHARACTERISTICS BY SYSTEMS OF MATING

Mating systems Year	No. ewes bred	Viability of ewes to lambing	Fertility	Fecundity	Parturient ability	Viability	Net reproductive rate	lbs. lamb weaned per ewe bred
		(%)	(%)	(%)	(%)	(%)	(%)	(lb.)
Rambouillet - 1963								
Inbred Lines	172	97.5	78.8	134.9	95.8	80.5	77.5	55.7
Line-Cross	458	96.7	82.7	142.1	95.3	85.1	93.0	70.1
Topcross	429	98.4	84.3	152.7	95.6	86.4	104.9	81.9
Selected Control	180	98.9	94.4	139.3	97.4	89.0	112.8	86.7
Stabilized Control	101	98.0	81.8	139.5	99.1	90.2	100.0	75.6
Targhee- - 1962+1964								
Inbred Lines	211	97.5	78.4	150.3	87.6	78.3	76.8	61.0
Line-Cross	855	96.6	81.5	153.9	91.1	87.0	95.8	78.1
Topcross	575	97.9	86.9	151.0	93.0	86.5	103.0	83.3
Selected Control	366	98.4	86.2	155.1	94.3	87.0	107.3	90.7
Stabilized Control	180	99.4	95.2	149.1	86.5	88.4	108.1	86.6
Columbia 1962+1964								
Inbred Lines	121	98.3	88.9	147.4	86.9	80.7	90.1	70.1
Line-Cross	520	96.7	82.0	154.6	91.0	84.5	95.2	81.0
Topcross	318	98.1	84.3	141.8	93.3	87.0	95.1	79.1
Selected Control	358	98.6	82.4	142.8	90.6	83.3	87.3	77.4
Stabilized Control	189	97.8	77.7	144.0	92.7	83.3	85.8	71.2

TABLE 13A. MEANS OF TOPCROSS ADJUSTED WEANLING TRAITS BY ORIGIN OF SIRE

Origin of Sire	Year	No. lambs weaned	Weaning weight (lb.)	Body type (sc.)	Body condition (sc.)	Staple length (cm.)	Face cover (sc.)	Neck folds (sc.)	Side grade (code)	Index
Rambouillet-1963										
Inbred Lines		450	72.4	2.70	2.82	4.49	3.68	1.31	2.23	133.1
Selected Control		18	74.7	2.66	2.70	4.66	3.20	1.05	2.50	145.5
Stabilized Control		24	74.5	2.58	2.76	4.86	3.74	1.22	2.44	137.1
Purchased		11	72.0	2.60	2.64	4.59	3.93	1.06	2.02	130.8
Recurrent Selection Lines		64	70.6	2.64	2.84	4.64	3.64	1.38	2.28	134.0
Targhee-1962+1964										
Inbred Lines		667	78.4	2.60	2.47	4.76	3.14	1.27	3.38	146.5
Selected Control		42	78.2	2.58	2.50	4.89	2.94	1.12	3.50	152.0
Stabilized Control		31	74.3	2.62	2.66	4.64	3.37	1.38	3.12	138.3
Purchased		29	79.1	2.57	2.43	4.42	3.42	1.40	3.15	138.8
Recurrent Selection Lines		101	77.8	2.62	2.46	4.65	3.26	1.33	3.19	142.7
Columbia-1962+1964										
Inbred Lines		303	78.9	2.50	2.43	4.87	3.22	1.26	3.66	131.6
Selected Control		33	77.0	2.64	2.60	4.82	3.31	1.18	3.73	130.2
Stabilized Control		38	76.2	2.50	2.48	4.94	3.23	1.16	3.79	129.2
Purchased		33	78.2	2.39	2.41	4.80	3.28	1.14	3.76	129.1

TABLE 13B. MEANS OF TOPCROSS REPRODUCTIVE CHARACTERISTICS BY ORIGIN OF SIRE

Origin of Sire	Year	No. ewes bred	Viability of ewes to lambing	Fertility	Fecundity	Parturient ability	Viability	Net reproductive rate	Lbs. lamb weaned per ewe bred
			(%)	(%)	(%)	(%)	(%)	(%)	(lb.)
Rambouillet	1963								
Inbred Line		429	98.4	84.3	152.7	95.6	86.4	104.9	81.9
Selected Control		16	93.8	86.7	176.9	100.0	78.3	112.5	89.3
Stabilized Control		16	100.0	93.8	160.0	100.0	100.0	150.0	119.3
Purchased		15	100.0	60.0	144.4	100.0	84.6	73.3	59.3
Recurrent Selection Lines		64	98.4	89.1	143.2	93.9	85.3	100.0	78.7
Targhee -	1962+1964								
Inbred Line		639	97.8	87.4	151.6	93.3	86.6	104.6	84.4
Selected Control		32	100.0	96.9	161.0	93.8	87.1	128.1	99.7
Stabilized Control		32	90.6	89.2	140.3	92.9	85.3	96.9	76.7
Purchased		32	93.8	90.6	154.9	86.4	80.6	90.6	72.3
Recurrent Selection Lines		100	99.0	93.6	150.1	90.4	83.2	105.2	84.2
Columbia -	1962+1964								
Inbred Line		318	98.1	84.3	141.8	93.3	87.0	95.1	79.1
Selected Control		32	96.9	93.8	141.9	92.5	88.1	103.1	83.3
Stabilized Control		32	96.9	100.0	135.6	97.6	92.7	118.8	96.0
Purchased		32	100.0	90.6	131.2	97.4	89.9	103.1	89.2

TABLE 14A[1] PARTIAL REGRESSIONS OF ADJUSTED WEANLING TRAITS ON INBREEDING OF LAMB

Year	Weaning weight (lb.)	Body type (score)	Condition (score)	Staple length (cm.)	Face cover (score)	Neck folds (score)	Side grade (code)	Ave. daily gain (lb.)
				Rambouillet				
1959	-.259	.015	.032	.009	-.013	-.031	.006	
1960	-.310	.016	.021	-.001	-.012	-.003	-.001	
1961	-.189	.011	.017	-.003	-.024	-.011	-.004	
1962	-.030	.002	.003	-.001	.001	.001	-.00[illegible]	
1963	-.194	.010	.010	-.010	.020	.006	-.000	-.002
1964	-.276	.030	.030	-.011	.010	-.006	-.000	-.002
Average	-.210	.014	.019	-.003	-.003	-.007	.000	-.002
				Targhee				
1959	-.358	.025	.046	-.009	.043	-.001	-.025	
1960	-.264	.003	.026	-.003	-.029	.005	.003	
1961	-.132	.001	.004	-.000	-.001	-.009	-.032	
1962	-.174	.030	.040	.001	-.040	.000	.003	
1963	-.235	.010	.030	.002	.010	-.005	.020	-.002
1964	-.332	.030	.020	.006	-.050	-.025	.010	-.003
Average	-.249	.016	.028	-.001	-.011	-.006	-.004	-.002
				Columbia				
1959	-.143	.022	.028	-.010	.031	-.007	.003	
1960	-.403	.067	.054	-.032	.045	-.008	-.024	
1961	-.072	.003	.011	-.012	-.006	.005	-.002	
1962	.110	.010	.000	-.013	.040	.001	-.037	
1963	-.221	.020	.020	-.013	.030	-.001	-.010	-.002
1964	-.016	.020	.020	-.006	.040	-.021	-.000	-.000
Average	-.124	.024	.022	-.014	.030	-.005	-.012	-.001

TABLE $14A_2$. PARTIAL REGRESSIONS OF ADJUSTED WEANLING TRAITS ON INBREEDING OF DAM.

Year	Weaning weight (lb.)	Body type (score)	Condi- tion (score)	Staple length (cm.)	Face cover (score)	Neck folds (score)	Side grade (code)	Ave. daily gain (lb.)
				Rambouillet				
1959	-.136	.020	.000	-.014	.031	.016	-.007	
1960	-.093	.008	.007	-.009	.030	.008	-.002	
1961	-.045	-.002	-.006	-.002	.017	-.001	.004	
1962	-.183	.010	.010	-.002	.020	.011	-.000	
1963	-.228	.010	.010	-.004	.010	-.002	-.000	-.002
1964	-.061	-.010	-.000	.008	.010	.001	-.000	-.001
Ave.	-.124	.006	.004	-.004	.020	.006	-.001	-.002
				Targhee				
1959	-.046	.002	.008	.001	-.023	-.008	.011	
1960	-.174	.011	.010	-.001	.015	-.012	.004	
1961	-.207	.005	.011	.004	.011	-.001	.007	
1962	-.234	.020	.030	-.008	.010	-.005	-.000	
1963	-.044	.000	.010	.008	.000	.001	-.000	-.000
1964	-.166	.020	.020	-.003	-.000	-.008	.000	-.001
Ave.	-.145	.010	.015	.000	.002	-.006	.004	-.000
				Columbia				
1959	-.081	.007	.005	-.007	-.009	.021	-.013	
1960	-.018	-.004	.012	-.001	-.012	.007	.022	
1961	-.184	.008	.017	-.002	.026	.001	.002	
1962	-.109	.020	.030	-.013	.010	-.004	-.013	
1963	-.273	.020	.040	-.015	.040	.002	-.000	-.002
1964	-.249	.030	.050	-.008	.040	.019	-.000	-.002
Ave.	-.152	.014	.026	-.008	.016	.008	.000	-.002

TABLE 14B. TOTAL AND PARTIAL REGRESSIONS OF REPRODUCTIVE CHARACTERISTICS ON INBREEDING OF DAM AND LAMB

Inbr.	Fertility	Fecundity	Parturient ability	Viability	Net reproductive rate	Lbs. lamb weaned per ewe bred
			Total Regressions			
			Rambouillet			
Dam	-.244	-.547	-.138	-.255	-1.094	-1.039
Lamb			-.121	-.237	-1.016	-1.001
			Targhee			
Dam	-.179	.192	-.416	-.178	- .731	-1.011
Lamb			-.412	-.289	- .941	-1.110
			Columbia			
Dam	.184	-.609	-.079	.154	-.267	- .301
Lamb			.029	.086	-.629	- .632
			Partial Regressions			
			Rambouillet			
Dam			-.265	-.387	-1.654	-1.251
Lamb			.140	.144	.615	.233
			Targhee			
Dam			-.045	.983	1.860	.874
Lamb			-.371	-1.162	-2.593	-1.887
			Columbia			
Dam			-2.082	1.856	4.144	3.501
Lamb			2.698	-2.293	-5.941	-5.121

TABLE 15. WITHIN SIRE VARIANCE OF INBRED LINES AS A PERCENTAGE OF WITHIN SIRE VARIANCE OF NONINBRED GROUPS*

Traits	Rambouillet		Targhee		Columbia	
	Wean.	Yrlg.	Wean.	Yrlg.	Wean.	Yrlg.
Body weight	99.9	90.3	98.1	110.6	75.0	88.7
Face cover	141.9	106.4	118.5	101.9	129.7	108.4
Neck folds	72.2	80.9	96.2	106.1	103.0	95.2
Body type	124.0	122.4	106.5	120.7	91.8	93.4
Body condition	106.0	109.3	107.0	118.5	87.1	106.0
Staple length	84.6	86.9	93.2	88.5	106.7	92.9
Crimp	97.5	92.5	86.0	115.9	93.4	91.2
Side grade	109.7	96.1	98.0	102.9	97.9	108.6
Belly wool	83.0	85.9	95.5	96.9	108.6	97.9
Thigh grade	103.0	116.7	103.5	109.2	93.7	119.8
Thigh grade score	114.9	96.9	139.7	105.1	72.2	99.7
Index	109.8		112.4		83.9	
Birth weight	86.2		93.5		126.9	
ADG - Birth to weaning	101.0		112.6		74.5	
Shearing grade		108.2		89.6		110.5
Body width		111.3		112.7		113.1
Body depth		122.8		120.9		81.9
Height at withers		94.6		102.4		140.4
Width of shoulder		94.3		105.7		139.6
Circumference of chest		102.0		89.3		113.9
ADG - weaning to yearling		85.8		95.3		96.5
Wool diameter grade		135.1		106.1		105.6
Clean fleece weight		80.9		85.2		86.1
Fiber diameter		117.5		111.8		103.7
Grease fleece weight		95.5		93.7		89.1
Var. in fiber diameter		101.3		115.3		100.8
Percent clean yield		89.1		97.4		105.3
Length of body		104.4		111.9		109.0
Average	102.4	101.1	104.3	104.5	96.0	103.9

* Average percent inbreeding of Rambouillet, Targhee and Columbia ewes is 21.7, 17.3 and 22.0, respectively.

THE PLACE OF INBREEDING RESEARCH WITH SHEEP?

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One question that we must attempt to answer in a rational manner is: What place does the development, propagation and evaluation of inbred lines of sheep have in the total genetic and breeding research program with sheep? Perhaps an answer to this question would be of value to those working with other species. Critical research on inbreeding effects and heterosis effects will provide much understanding of a portion of the biology involved. Whether or not we can see a practical application in the industry just now, other than in top crossing, is not the primary question. If the facts are made well known through effective research their usefulness to the industry can be worked out later, perhaps 50 or 100 years hence. Other questions are of some immediate and practical interest to researchers who are involved in inbreeding research: What should be done with existing lines? How many lines should be preserved? Should only a few "superior" lines be retained from the present number and continued on indefinitely? Should new lines be formed and the long, tedious inbreeding cycle be repeated? What are the traits or characteristics that should be observed?

Inbred lines such as those at Dubois with average inbreeding coefficients on the order of 20 to 40% are expected to have greater homozygosity than existed in the general population from which they were derived. Hence, there is somewhat less opportunity for intra-line selection to be effective in moving such lines to higher levels of genetic merit. On the other hand, since the rate of inbreeding is relatively slow in sheep intra-line selection has opportunity to alter the consequences of inbreeding. Some questions to be answered from a practical point of view are: To what extent can line improvement be accomplished by intra-line selection carried on concurrently with inbreeding? Will both a higher level of breeding value and greater prepotency result? To what extent is heterosis involved? In application we would like to achieve higher phenotypic line merit, higher breeding values in top-cross matings, and higher prepotency. Phenotypic merit of the inbred lines, except for fertility, probably is the least important. More important, however, we wish to know how and why the goals are achieved and the factors involved.

Experiments involving both selection and inbreeding, either together or separately, can most satisfactorily be accomplished with reference to certain other breeding systems in which adequate control groups are maintained. We have established genetically stabilized control groups (unselected and non-inbred) and groups that are being selected for high overall merit in each breed. We intend to provide more adequate stabilized controls and to set up breeding groups which are selected for single traits, avoiding inbreeding. Our immediate problem is what to do with the inbred lines following the present testing program.

It is difficult to evaluate just where we are in the inbreeding program at Dubois. We now have 27 breeding groups in the Rambouillet breed, 18 in the Targhee, and 10 in the Columbia which are referred to as inbred lines. Several of these are not highly enough inbred to justify designation as inbred lines. The program of line evaluation in which top-cross and line-cross matings are made will provide data on which to evaluate the general combining ability of each line in a reasonably satisfactory fashion. In addition to this information on general combining ability we have substantial data on the phenotypic merit of the inbred lines themselves. So far as industry application is concerned these two sources of information should provide suitable information for selecting lines for further investigation and research. The industry's use of inbred stock most likely would be based on top-cross merit. At present there would be limited opportunity for the industry to exploit any heterosis that may be found among line-crosses on an intra-breed basis. Cross breeding has a definite place in sheep breeding programs. However the heterosis obtained from breed crosses using non-inbred stocks may be quite different from any obtained in intra-breed line-crosses, or from the use of inbred stocks in breed crosses. This is an area for future research and should be considered in long range plans involving cross-breeding.

The breeding groups at Dubois which are referred to as inbred lines, probably represent a wide cross section of the three breeds involved. With but few exceptions, selection has been practiced on an intra-line basis. Very few lines have been culled, therefore within the framework of the breeds involved we are probably still working with near maximum genetic variance. If the selection that has been practiced has not altered the primary effects of inbreeding we might speculate that genetic variance has in fact been increased as a result of the inbreeding program. This assumption is probably not too unreasonable because efforts in selection within the inbred lines have been feeble due primarily to the small size of the lines and variation in selection criteria from one line to another. It is suggested that in the operational phase where inbred lines are culled that attention be given primarily to reproductive performance of the lines themselves and to their general combining ability for total merit.

The reason for this suggestion is that we have much more information in these two categories than in any other. Evidence on specific combining ability will be limited, telling us only in a general way whether or not it may be important, and hopefully we will obtain some idea of the relative fraction of the total genetic variance that is accounted for by specific effects.

Selection of a few lines on the basis of line merit and general combining ability should provide highly productive sheep for further research. We would expect the additive genetic variance to be reduced if selection is at all intense and effective. If we find that specific combining ability is of some importance in these tests, will it become of even greater importance, relatively speaking, after selection for general combining ability has been accomplished? Will the few surviving inbred lines after such selection provide suitable experimental material for studies of heterosis effects among inbred lines within breeds and methods of exploiting this source of genetic diversity? Should inbred lines for future research be selected at random from existing inbred lines?

We now have some estimates of gene frequency of blood group alleles in sheep. Evidence concerning correlation between blood group alleles and phenotypic merit is meager. It would appear wise to follow the course of any future inbreeding and selection programs with periodic checks on blood group gene frequencies. This will provide basic information to some extent on what is happening at the gene level and information on relationships between these genes and production. There may be other physiological characteristics of the organism that have relatively simple genetic explanations that can be studied by such techniques as electrophoresis.

Selection goals in future research should be oriented toward some of the more fundamental components of total economic merit. These would include prolificacy, viability, growth rate and maternal ability. The characteristics of the lamb carcass is also another highly important factor in sheep production. Research in furthering our understanding of the formation of the various tissues (bone, muscle and fat) are essential to progress in the application of breeding methods for improving this end product.

Ewe productivity, total weight of lambs per ewe or more basically weight of lambs per 100 pounds of ewe, depends on ovulation rate, fertilization rate, survival of zygote to weaning age and unit weight of the lambs at weaning. The number of lambs produced per ewe or prolificacy is generally considered to be lowly heritable yet some components of reproduction are adversely affected by inbreeding. Little is known about hereditary factors involved in embryonic death. It is known to occur in sheep, usually before the 35th day of gestation. Prenatal growth as measured by birth weight is adversely affected

by inbreeding and favorably affected by cross breeding. Birth weight also is moderately heritable (about 30 percent). Postnatal growth rate of individual lambs is about 25 percent heritable, but it depends also on such factors as milk supply of the dam, competition from siblings in the case of multiple births, etc. some of which are or may be influenced by heredity. With the trend toward early weaning, 60 - 90 days of age, in which the economics are affected more by number of lambs per ewe rather than by market grade and weight of lamb at weaning increased attention needs to be given to the hereditary aspects of reproduction. This must be studied on the basis of its component parts - ovulation rate, fertilization rate, and embryo survival.

EXPERIMENTS ON INBREEDING AND LINE-CROSSING SWINE AT BELTSVILLE, MARYLAND, AND MILES CITY, MONTANA

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Early Studies on Inbreeding

An inbreeding experiment with swine was started by the former Bureau of Animal Industry at Beltsville in 1923. The purposes of this experiment were to study the effects of continued inbreeding and to develop strains for use in further breeding work. The experiment was started with several unrelated pairs of animals in the Poland China and Tamworth breeds. In 1924, three lines of Chester Whites were added. All lines were started by use of full-brother-sister matings. Improvement of the lines was to be accomplished by discarding the undesirable and multiplying the good either by further inbreeding or by crossing with other inbred lines possessing the desirable characteristics. The experiment with Poland China was discontinued after the second generation because of a decrease in fertility and high mortality.

One Chester White line was carried through seven consecutive generations of full-brother-sister matings, while one Tamworth line was inbred for five generations. Comparison between inbred and outbred Chester Whites showed litter weight at 70 days of age averaging 159 pounds for sixth generation inbred sows and 209 pounds for outbred sows. In the Tamworth inbred line the average litter weight at 70 days was only 89 pounds. Although the inbreds appeared to be more uniform in type and carcass quality, this advantage was not considered sufficient to counteract the disadvantages of fewer pigs in litters, higher mortality, slower gain, and greater feed requirements. Because of these detrimental inbreeding effects, the Tamworth line was discontinued in 1933. The Chester White line, on the other hand, was reconstituted by combining it with outbreds and inbreds of another line. A milder form of inbreeding than full brother and sister was used in this line until 1946 when it was transferred to the University of Wisconsin for studies in connection with the Regional Swine Breeding Laboratory with headquarters at Ames, Iowa. Results of the inbreeding work with the Chester White and Tamworth breeds are summarized in the annual reports of the Chief of the Bureau of Animal Industry for the years 1932-1935. A more detailed report of the effects of inbreeding on litter size in the Chester White line appeared in 1940.

Inbred Lines of Crossbred Origin

A new start in developing superior inbred lines of swine was made in 1934 when the Department in cooperation with the Iowa

Agricultural Experiment Station imported a group of seven boars and sixteen gilts of the Danish Landrace breed and two boars and four gilts of the Danish Yorkshire breed. In addition, two boars and two sows of the Large Black breed were imported from England in 1936. The primary purpose of these importations was to determine the feasibility of synthesizing new strains of swine, combining a maximum of the length of body and plumpness of ham of the Danish Landrace with certain desirable characters of other breeds, particularly their greater resistance to sun scalding and better overall performance under American feeding and management practices. Altogether, seven inbred lines were started at Beltsville from crossbred foundations involving the Landrace or Yorkshire as a parent breed. Of the seven lines, one line each was started in 1935 from crosses of the Danish Landrace with representatives of the Chester White (L-CW), Duroc (L-D), and Poland China (L-PC) breeds, one in 1936 from a Danish Yorkshire × Duroc cross (Y-D), and one in 1937 from a Danish Landrace × Large Black (L-LB) cross. The remaining two lines were started in 1940 from a Landrace × Hampshire cross that had been made at Miles City, Montana, with stock from each of the Landrace-Duroc (L-D-H) and the Yorkshire Duroc (Y-D-L-H) lines. In addition one purebred Landrace (L) line was maintained as a control and for grading-up purposes. All lines but the Y-D line were in existence until 1953 when the project was terminated. The Y-D line was dropped in 1945 because of poor performance and is not considered further here. Following the pattern used in the development of the Beltsville lines, one line of Landrace × Hampshire (L-H) breeding was started at Miles City in 1937.

Because of the greater susceptibility of white pigs to sun scalding, the plan in each case was to develop lines which would possess the coat color of their respective colored parent breed rather than the white hair coat of the Landrace or Yorkshire. To achieve this objective, first-cross pigs selected for breeding from matings involving the Duroc, Large Black, or Poland China breeds were used only for inter se matings or for backcrossing to their respective colored parent breed to assure the continued production of pigs with the desired color pattern. Thereafter, the general plan was basically one of backcrossing properly colored segregates to the Landrace or Yorkshire (or to L-D or Y-D animals in the case of the L-D-H and Y-D-L-H lines) and to alternate this system of topcrossing with inter se matings between animals saved from the last generation. The breeding plans generally followed in the development of the L-D, L-LB, L-PC, L-D-H, and Y-D-L-H lines are illustrated in figure 1 for the L-PC line.

[illegible] ... by Joseph (Crook) [illegible] ... Tennessee [illegible]

[illegible] ... the Chester White [illegible] ... and was in 1887 [illegible] ... In addition [illegible] ... in the United States [illegible] ... (1931).

Because of the greater [illegible] ... the first of their respective [illegible] ... Yorkshire [illegible] ... feeding [illegible]

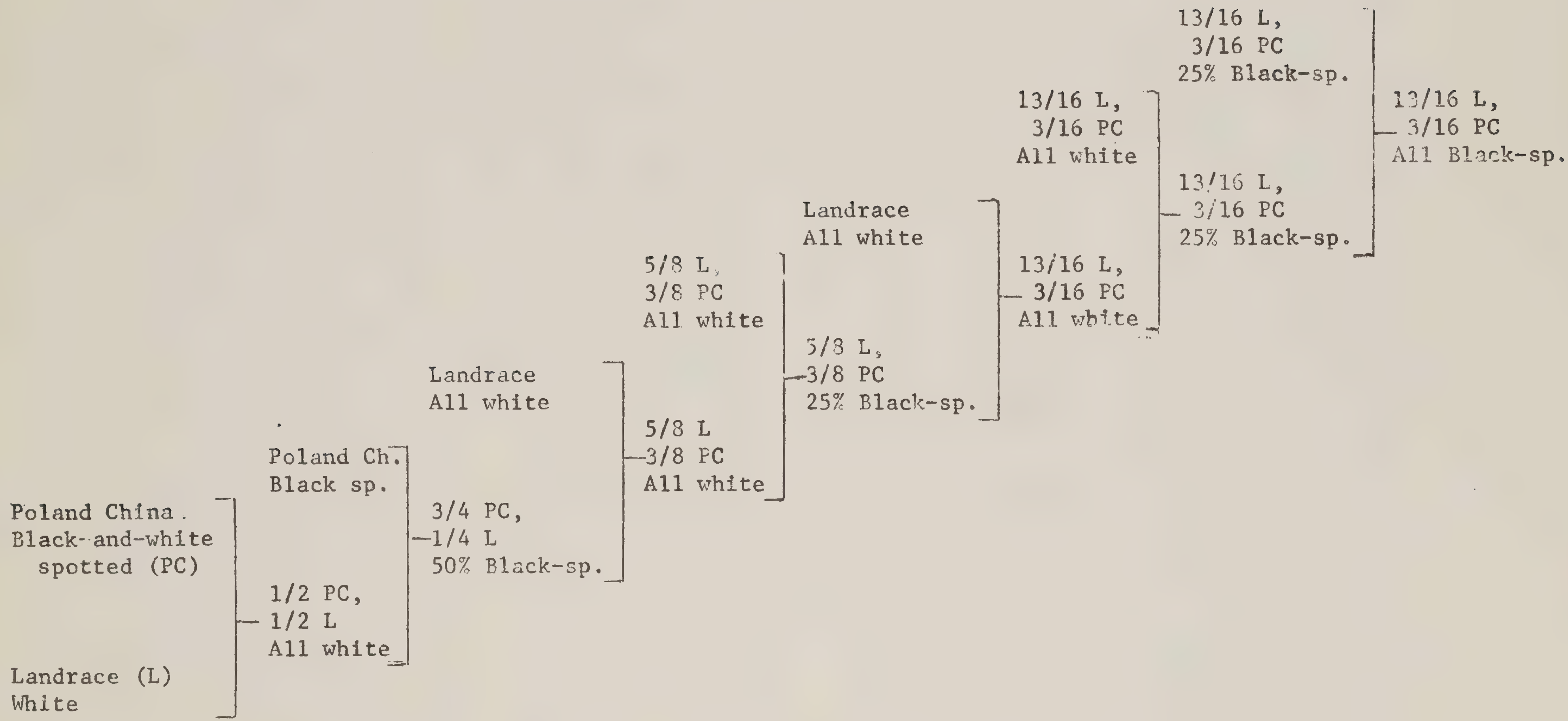


Figure 1. Breeding plans used in development of Beltsville No. 1 swine

The numbers of foundation matings of the stocks used in establishing the various inbred lines are shown in table 1 with their estimated percentage contribution to the 1951 pig crop. Generally from two to five boars were used to produce litters in each strain in the spring and fall of each year, and each boar was mated to a representative group of two to five females varying in age and relationship to their mates. The traits primarily considered in the selection of breeding stock were sow productivity as measured by litter size and litter weight at birth and at weaning, rate of growth, and carcass quality as reflected by the meat type conformation of the Landrace.

Beginning in 1938, stock from some of the lines was released to commercial breeders and State experiment stations to evaluate their usefulness under different environmental conditions. The L-PC line was closed to outside blood in 1942, followed by the L-CW and L-D lines in 1943, the L-D-H line in 1944, the L-LB line in 1945, and the Y-D-L-H line in 1947. The L-PC and Y-D-L-H lines were admitted to the Inbred Livestock Registry Association in 1951 and 1952, respectively, and renamed the Beltsville No. 1 and Beltsville No. 2 breeds. The L-H line developed at Miles City, Montana, was renamed Montana No. 1 when it was recognized as a breed in 1948.

The average coefficients of inbreeding and relationship among the six Beltsville lines tracing to crossbred foundations are shown in table 2 for the three years 1947, 1948, and 1950. Table 3 shows the number of males and females used in the development of the same six lines, while table 4 gives the numbers that contributed to the 1951 pig crop. As shown in figure 2, the average increase in inbreeding coefficients per year varied from 3.0 percent in the L-D-H line to 1.9 percent in the Landrace and L-D lines. In 1951, the average inbreeding coefficients of the L, L-CW, L-D, L-LB, L-PC, L-D-H, and Y-D-L-H lines were 33.3, 50.2, 31.1, 26.2, 34.2, 32.3, and 36.8 percent, respectively.

The yearly means for litter size at birth, litter size at weaning, and litter weight at weaning are plotted in figures 3 and 4 for the Beltsville lines with line means weighted by number of litters, including the Landrace line. There was a fairly uniform decline in each of the three traits, with the decline for the seven lines combined averaging 0.07 pigs per year for litter size at birth, 0.08 pigs for litter size at weaning, and 4.7 pounds for litter weight at weaning. A comparison among the regressions calculated for the different lines shows that all lines derived from crossbred foundations showed a downward trend in each of the traits studied, whereas only in the case of litter size at birth did the Landrace line also show a downward trend. While these differences between the Landrace and the other lines no doubt are partly due to the somewhat higher

Table 1. Source of inbred lines based on crossbred foundations and estimated percentage contribution of breeds to inbred lines in 1951[1]

Line	Year established	Number of foundation matings	Percent contribution from parent breeds						
			L	CW	D	H	LB	PC	Y
L-CW	1935	7	17	83	-	-	-	-	-
L-D	1935	21	75	-	25	-	-	-	-
L-LB	1937	8	75	-	-	-	25	-	-
L-PC	1935	17	74	-	-	-	-	26	-
L-D-H	1940	9	74	-	17	9	-	-	-
Y-D-L-H	1940	2	6	-	30	6	-	-	58

[1]CW = Chester White; D = Duroc; H = Hampshire; L = Landrace; LB = Large Black; PC = Poland China; Y = Yorkshire

Table 2. Average coefficients of inbreeding and relationship among inbred lines, for the 3 years 1947, 1948, and 1950

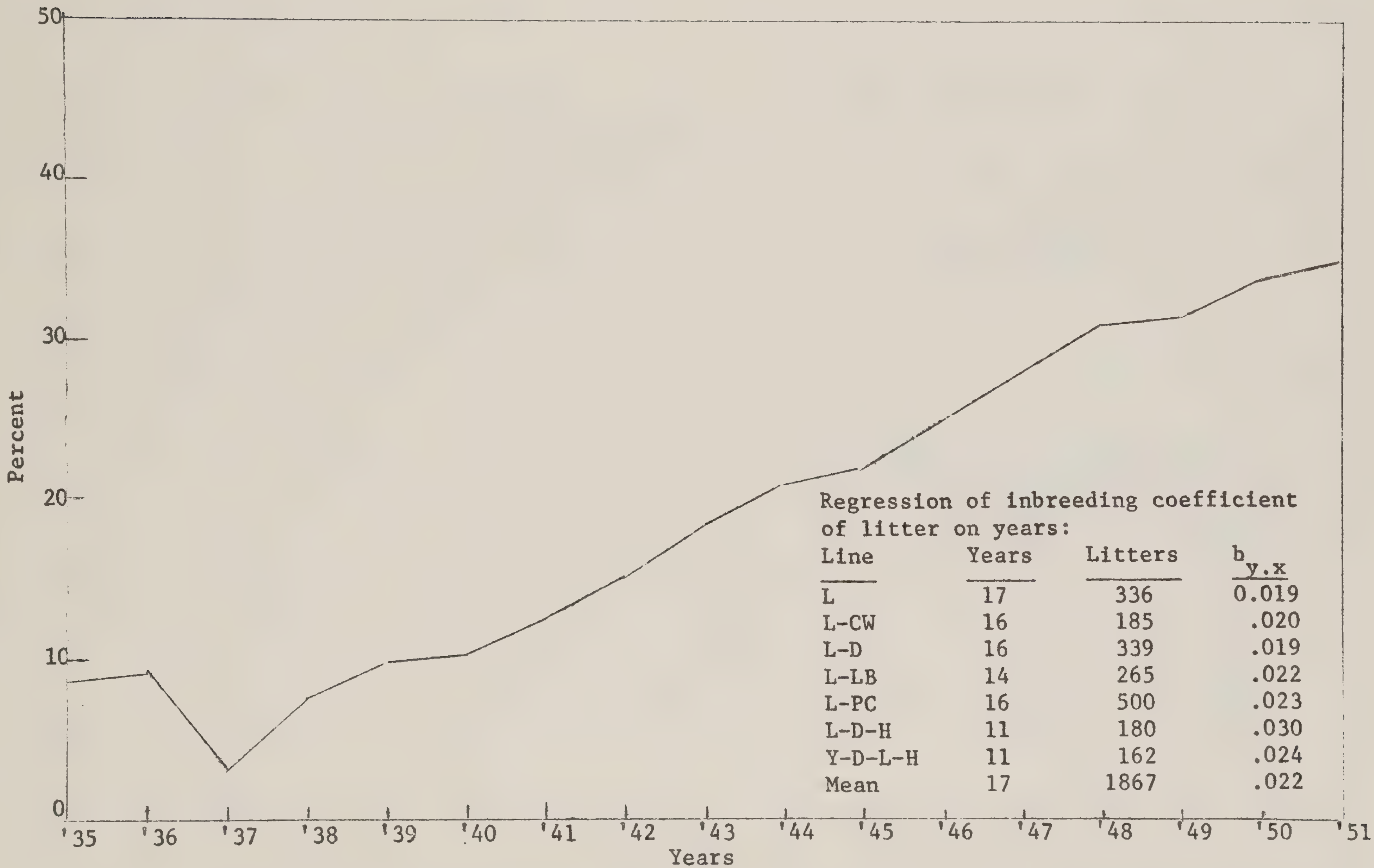
Line	Inbreeding coefficient	Relationship coefficient				
		L-D	L-LB	L-PC	L-D-H	Y-D-L-H
L-CW	0.411	0.012	0.018	0.014	0.020	0.000
L-D	.198	--------	.140	.135	.246	.018
L-LB	.187	--------	--------	.123	.121	.000
L-PC	.248	--------	--------	--------	.108	.000
L-D-H	.263	--------	--------	--------	--------	.031
Y-D-L-H	.283	--------	--------	--------	--------	--------

Table 3. Number of males and females of different breeds used in development of inbred lines

Line	Parent breed													
	L		CW		D		H		LB		PC		Y	
	M	F	M	F	M	F	M	F	M	F	M	F	M	F
L-CW	4	1	8	16	-	-	-	-	-	-	-	-	-	-
L-D	15	23	-	-	6	2	-	-	-	-	-	-	-	-
L-LB	19	17	-	-	-	-	-	-	3	2	-	-	-	-
L-PC	18	20	-	-	-	-	-	-	-	-	5	-	-	-
L-D-H	12	10	-	-	4	-	2	-	-	-	-	-	-	-
Y-D-L-H	-	2	-	-	2	-	2	-	-	-	-	-	4	2

Table 4. Number of males and females of different breeds that contributed to the inbred lines in 1951

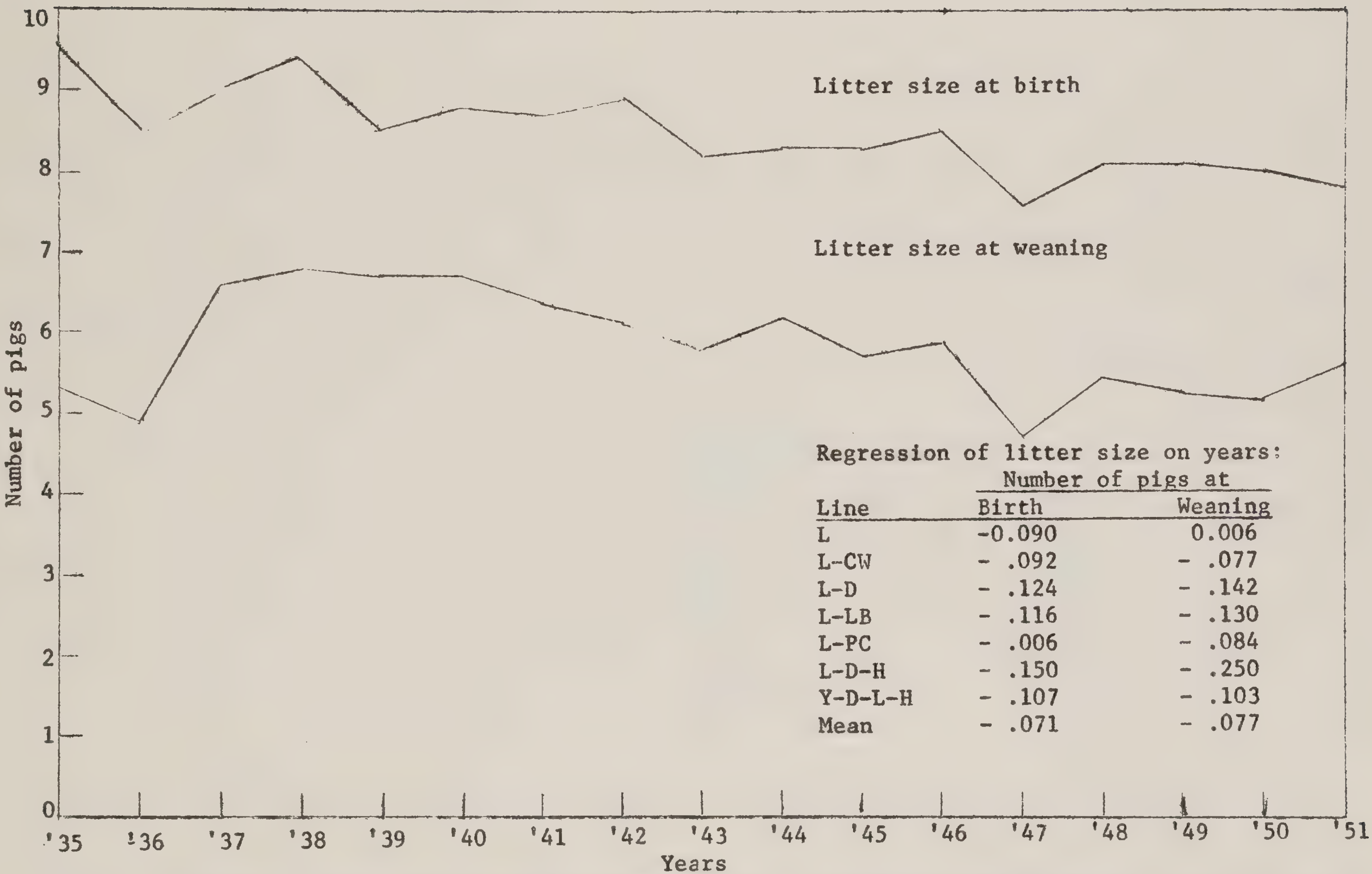
Line	Parent breed													
	L		CW		D		H		LB		PC		Y	
	M	F	M	F	M	F	M	F	M	F	M	F	M	F
L-CW	2	1	3	8	-	-	-	-	-	-	-	-	-	-
L-D	9	8	-	-	4	-	-	-	-	-	-	-	-	-
L-LB	8	5	-	-	-	-	-	-	2	1	-	-	-	-
L-PC	7	6	-	-	-	-	-	-	-	-	3	-	-	-
L-D-H	8	6	-	-	3	-	2	-	-	-	-	-	-	-
Y-D-L-H	-	2	-	-	2	-	2	-	-	-	-	-	4	2



Regression of inbreeding coefficient of litter on years:

Line	Years	Litters	$b_{y.x}$
L	17	336	0.019
L-CW	16	185	.020
L-D	16	339	.019
L-LB	14	265	.022
L-PC	16	500	.023
L-D-H	11	180	.030
Y-D-L-H	11	162	.024
Mean	17	1867	.022

Figure 2. Average percent inbreeding of litters in seven Beltsville lines by years



Regression of litter size on years:

Line	Number of pigs at Birth	Number of pigs at Weaning
L	-0.090	0.006
L-CW	- .092	- .077
L-D	- .124	- .142
L-LB	- .116	- .130
L-PC	- .006	- .084
L-D-H	- .150	- .250
Y-D-L-H	- .107	- .103
Mean	- .071	- .077

Figure 3. Average litter size at birth and at weaning in seven Beltsville lines by years adjusted to gilt basis

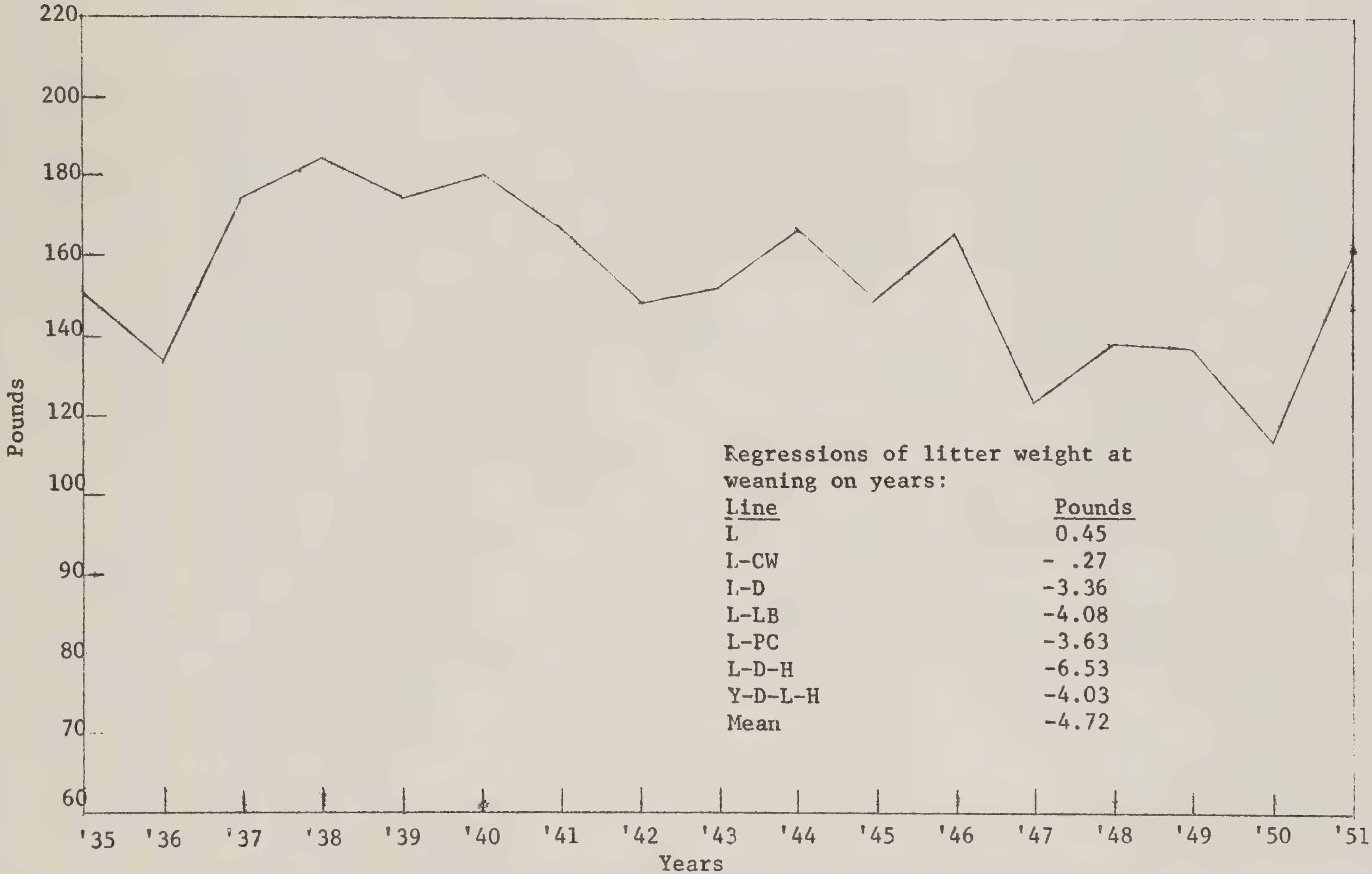


Figure 4. Average litter weight at weaning in seven Beltsville lines by years adjusted to gilt basis

inbreeding increase in the lines of crossbred origin, line differences in inbreeding effects probably are also partly responsible. This latter suggestion is supported by the fact that while intraseason regressions on inbreeding of dam and inbreeding of litter were negative for the most part, those obtained for the lines of crossbred origin were generally larger than those for the Landrace. Accordingly, opportunity for selection aimed at offsetting deleterious inbreeding effects would naturally have tended to be greater for the Landrace line than for the lines of crossbred origin. Postweaning growth data have not been analyzed in detail, but examination of the original data shows that both 140-day weight and daily gain to a live weight of about 225 pounds improved slightly in most lines.

Performance of Line Crosses

Studies designed to determine the crossing value of the Beltsville lines were started in 1947 when matings representing all the 30 possible reciprocal crosses among the L-CW, L-D, L-LB, L-PC, L-D-H, and Y-D-L-H lines, as well as matings within each line were made for fall litters. The same matings were repeated for fall 1948 litters, giving a total of 35 inbred litters and 184 single-cross litters for the analysis. The amounts of heterosis exhibited by the crosses is demonstrated graphically in figure 5, where the range in superiority or inferiority of the 15 pairs of reciprocal crosses is shown as a percentage of the mean for their respective parent lines. In general, both prenatal and postnatal mortality were lower among crosses than among inbreds, and crosses tended to grow a little faster than inbreds while both groups were suckling inbred sows. In litter size, crosses exceeded inbreds by 1.2 pigs per litter or 14 percent at birth, and by 1.7 pigs or 29 percent at 56 days. In litter weight, crosses exceeded inbreds by 2.4 pounds or 10 percent at birth, and by 64 pounds or 40 percent at weaning. Crosses averaged a little lighter at birth than inbreds; but crosses exceeded inbreds by 2.7 pounds or 10 percent at 56 days, and by 9.3 pounds or 6 percent at 140 days. Even though the dams of these single crosses were about 25 percent inbred, their performance appears to average as good as that of most outbreds reported in the literature. The results suggest therefore that developing superior inbred lines with varying genetic backgrounds and using the best of such lines for crossing offer opportunity for surpassing the performance of conventionally bred hogs.

Performance of Inbred Lines in Crosses with Purebreds

Results illustrating the heterosis shown by crossbred pigs as well as that shown by crossbred sows as dams are available from an

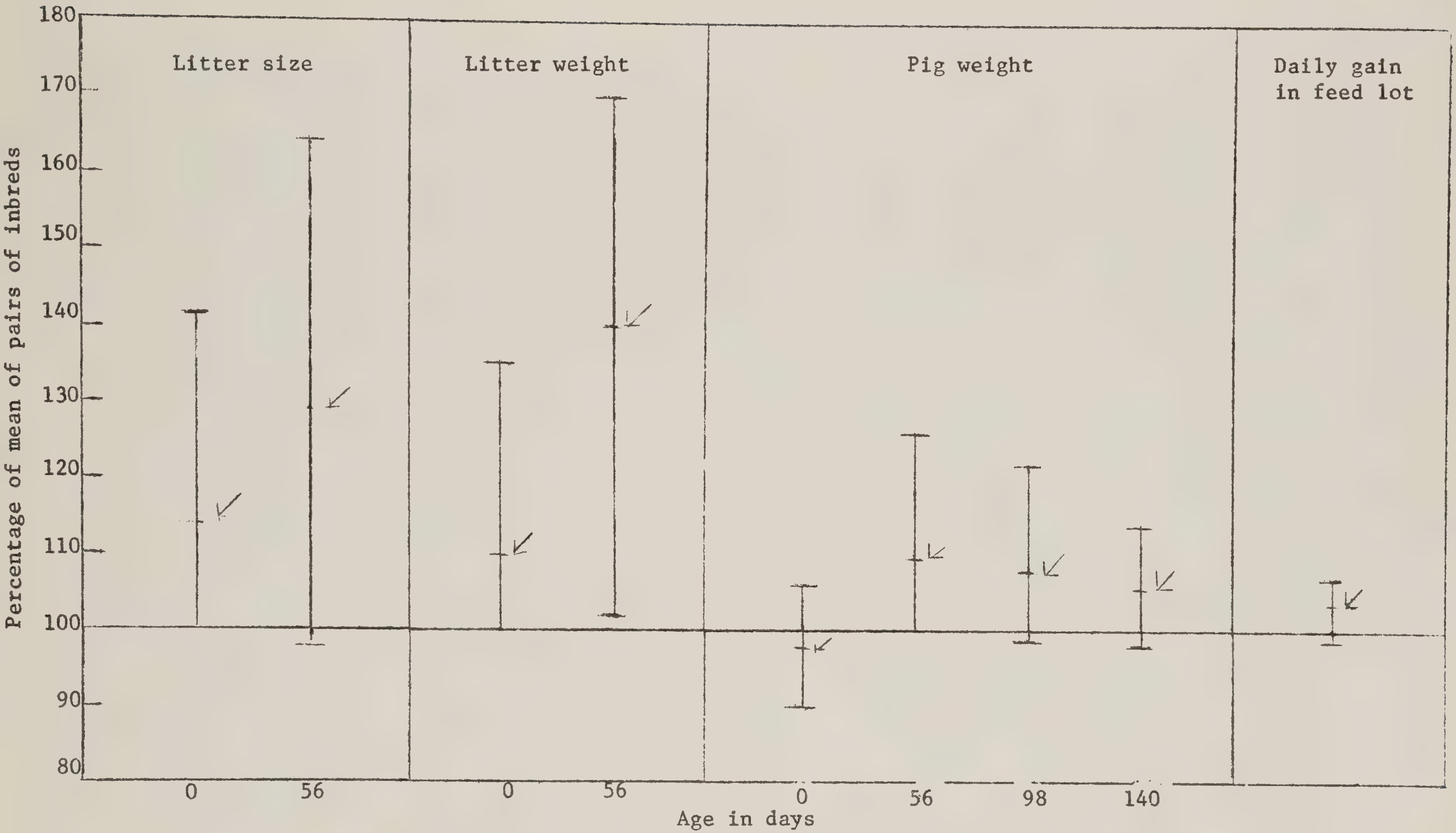


Figure 5. Range in performance of 15 pairs of reciprocal crosses as percentage of means of corresponding inbred parent stocks (arrows indicate means for all crosses). Beltsville data.

experiment conducted at Beltsville during the years 1952 and 1953. The 407 litters available for study included 35 noninbred purebred litters from four breeds; 88 inbred litters from six of the seven Beltsville lines referred to above; 90 single-cross litters representing 24 different combinations sired by boars of the four pure breeds and out of sows from the six inbred lines; and 194 second-cross litters sired by various combinations of noninbred purebred and inbred boars and out of single-cross sows. Figure 6 summarizes the pertinent results for the four kinds of pigs.

Single crosses exceeded inbreds by 0.5 pigs or 6 percent in litter size at birth, by 0.9 pigs or 16 percent in litter size at weaning, and by 57 pounds or 32 percent in total litter weight at weaning. Crosses were also heavier than inbreds at 140 days and required about 7 percent less feed than inbreds for 100 pounds gain from weaning to 225 pounds. In each of the five traits studied, single crosses also averaged as good as or better than noninbred purebreds despite the fact that the dams of single-cross litters were 34 percent inbred, as compared with 0 percent for dams of purebred litters.

The added advantage of utilizing the heterosis ususally shown by crossbred dams for maternal traits is illustrated by the performance of second-cross compared with first-cross litters. As shown in figure 6, second crosses exceeded first crosses by 1.4 pig or 17 percent in litter size at birth, by 1.0 pig or 16 percent in litter size at weaning, and by 33 pounds or 14 percent in litter weight at weaning. Compared with inbreds and noninbred purebreds, the superiority shown by second crosses averaged 25 and 17 percent for litter size at birth, 34 and 23 percent for litter size at weaning, and 51 and 30 percent for litter weight at weaning. These results demonstrate clearly that the benefits from crossbreeding are likely to be greatest when the hybrid vigor exhibited by maternal traits in the crossbred sow is also utilized. As was to be expected, postweaning growth rate, as measured by 140-day weight and feed efficiency from weaning to a final weight of 225 pounds, differed little between second and first crosses.

Performance of Beltsville Lines in Crosses on Pennsylvania Farms

Tests designed to evaluate the combining ability of the Beltsville lines under conventional farm conditions were conducted during the years 1950 and 1951 in cooperation with 28 Pennsylvania farms. Specifically, the plan of these tests was to compare topcross progeny, produced by using inbred boars from the Beltsville lines on purebred gilts, with the progeny of purebred matings on the same farms. A limited amount of information was also obtained on the performance of topcross and purebred gilts in 1952 and 1953. Records were available on 227 purebred litters and 238 topcross

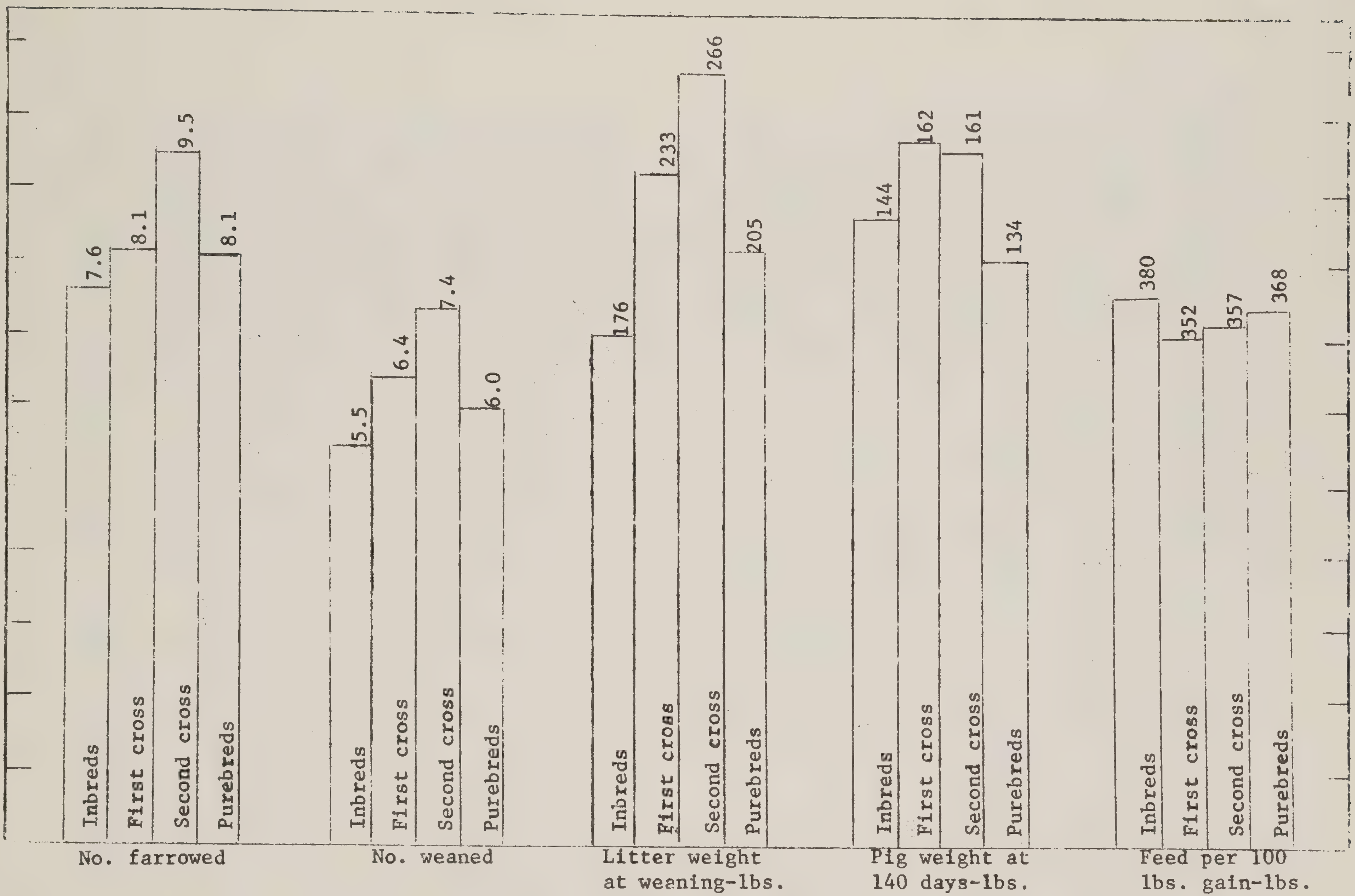


Figure 6. Comparison of inbreds and noninbred purebreds with first cross out of inbred sows and by noninbred boars and second cross out of first cross sows and by inbred and noninbred boars. Litter data adjusted to a gilt basis (Beltsville, Maryland, 1952-1953).

litters at birth and weaning, on 1,051 purebred and topcross pigs in the feedlot, and on 959 carcasses. The topcross progeny were out of purebred gilts of four breeds and were sired by boars from seven inbred lines. The results for the first two years gave no indication that topcrossing of inbred boars on purebred sows would increase the number of pigs in the litter at farrowing or weaning. However, topcrosses exceeded purebreds by 26 pounds or 18 percent in litter weight at weaning and by 20 pounds or 17 percent in individual 140-day weight. Both differences were highly significant. The most striking feature of the results was the superiority of the topcross gilts over the purebred gilts in litter production. In litter size at weaning, for example, topcross gilts exceeded purebred gilts by 2.6 pigs or 49 percent. The advantage for topcross gilts in litter weight at weaning was 112 pounds or about 95 percent. These results were taken from a Ph. D. thesis submitted by Estel Cobb to Iowa State University in 1958. His results for the performance of topcross gilts agree favorably with those obtained for single-cross gilts from the reciprocal crosses made at Beltsville. In order to maximize the benefits from crossbreeding, it would seem therefore that inbred lines would be most valuable in some sort of rotational crossing scheme in which the crossbred gilts are retained in the herd to produce the female stock for the next generation.

Inbreeding and Line-Crossing Tests at Miles City

As was noted above, a line of Landrace-Hampshire breeding was started at Miles City in 1937. The breeding plans used in the development of this line were essentially the same as those used at Beltsville. The line was closed to outside blood in 1940 and the estimated percentage of blood that year was about 58 percent Landrace and 42 percent Hampshire. In 1947, the line was subdivided into six one-sire lines and one two-sire line. Two one-sire lines were discontinued in 1950 and 1951 because of poor performance. The others were maintained as separate lines until 1954 when the experiment was terminated. The average inbreeding in 1954 was 66 percent for the one-sire lines and 55 percent for the two-sire line. Figure 7 gives the means for three litter traits by years. Both litter size and litter weight declined somewhat more rapidly in the one-sire lines than in the two-sire line, due presumably to the higher inbreeding rates in the one-sire lines. Although the inbreeding in the Miles City lines was considerably higher than in the Beltsville lines, a comparison of the results in figure 7 with those in figures 3 and 4 strongly suggests the Miles City lines averaged at least as good as the Beltsville lines in each of the traits studied.

In 1951, matings representing all the 12 possible reciprocal crosses between four one-sire lines, as well as matings within each line,

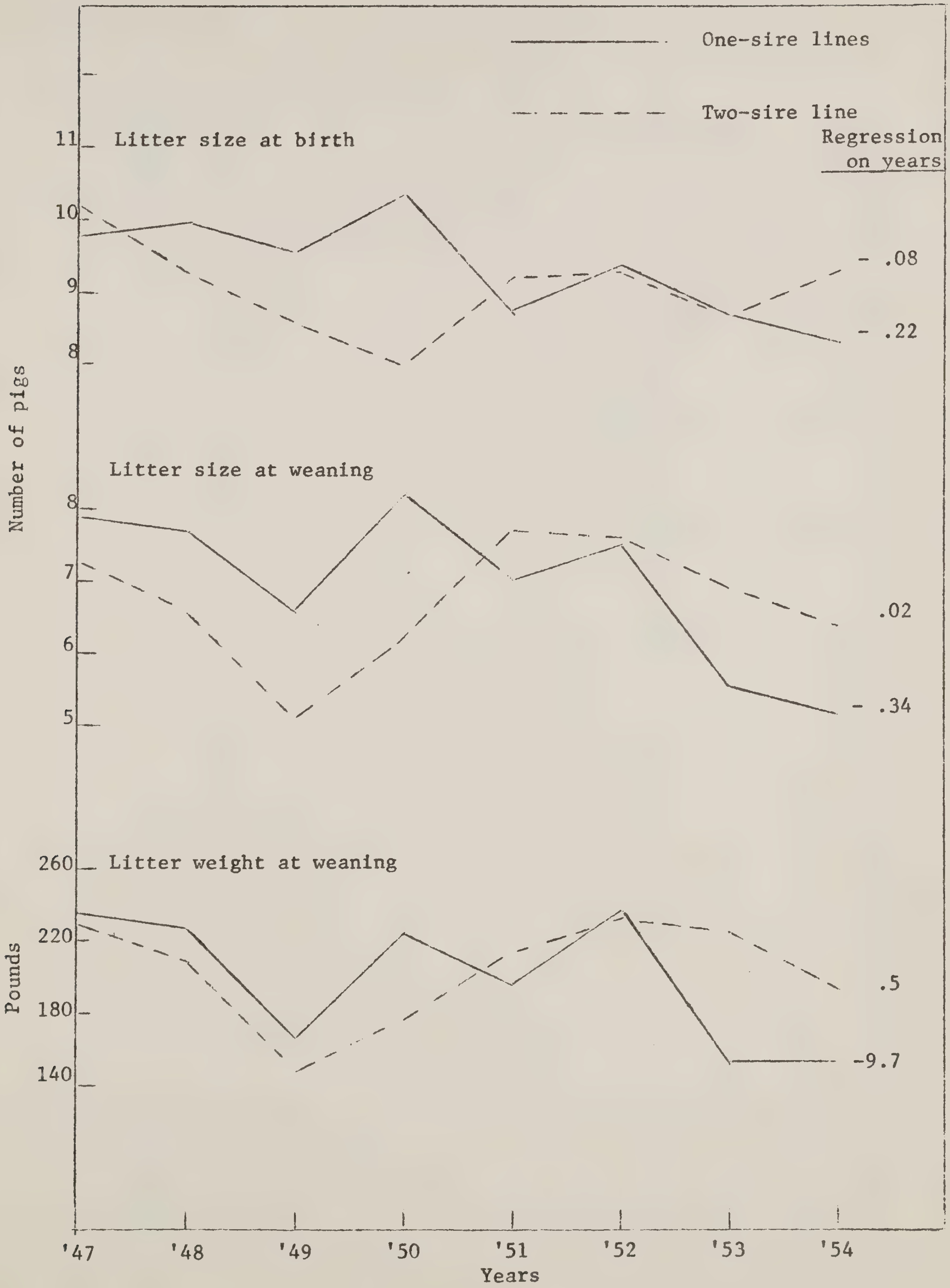


Figure 7. Average litter size and litter weight in one- and two-sire lines by years. Miles City data.

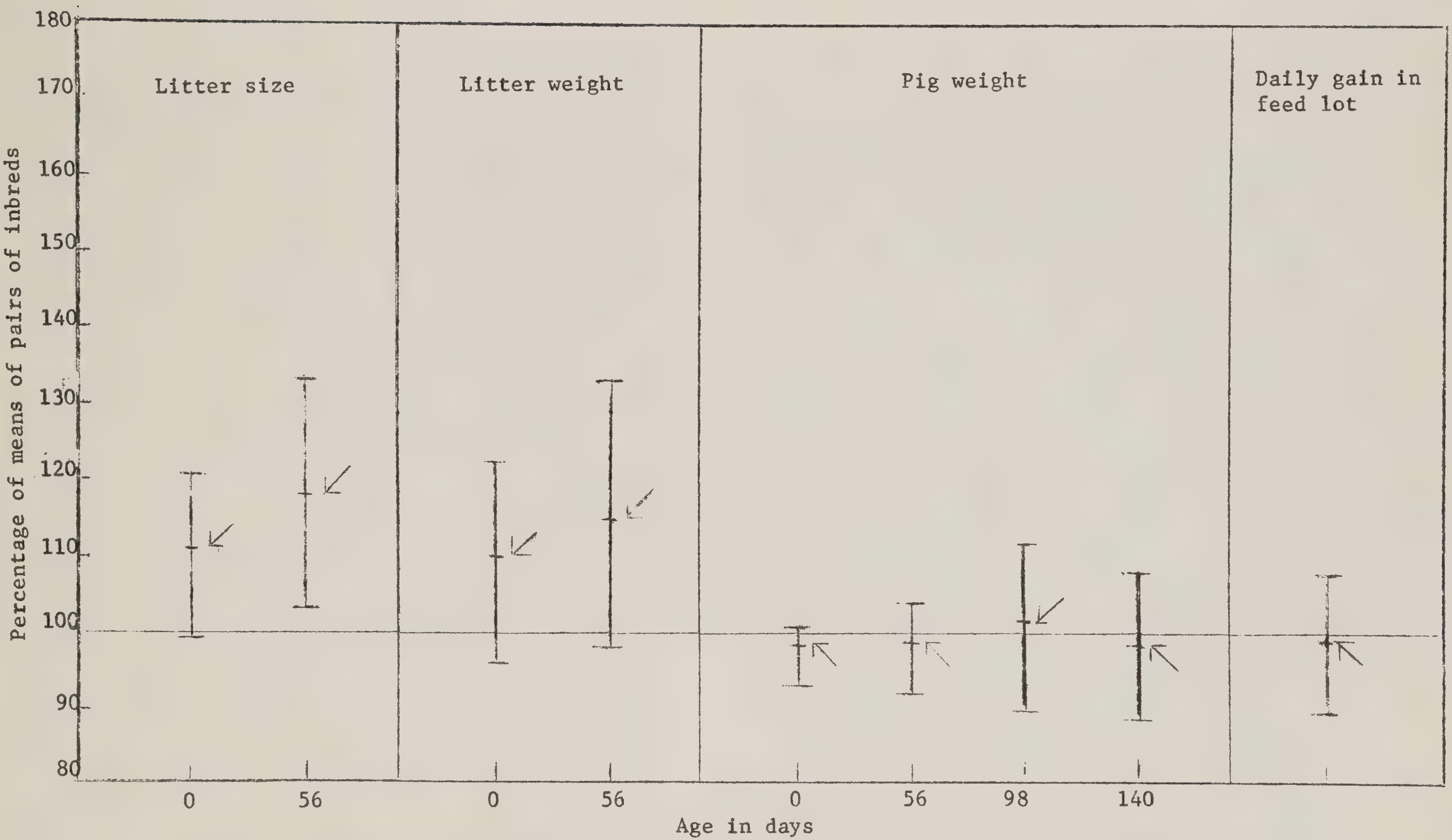


Figure 8. Range in performance of 6 pairs of reciprocal crosses as percentage of means of corresponding inbred parent stocks (arrows indicate means for all crosses). Miles City data.

were made for spring litters. The one-sire lines were represented by 14 litters and the single crosses by 49 litters. Information on the productivity of crossbred sows was obtained in 1952 by mating single-cross gilts with single-cross boars. A total of 52 three- and four-line cross litters and 14 inbred litters were available for this phase of the study. Figure 8 shows the performance of the single crosses as percentage of the means of corresponding parent lines. The amounts of heterosis exhibited by the various traits in figure 8 all appear to be somewhat lower than those reported for the crosses among the Beltsville lines. However, when we consider that the four lines represented in the Miles City crosses were rather highly related to each other, i.e., about 30 percent, the relatively high amounts of heterosis exhibited by some of the traits in the Miles City crosses are rather striking. In litter weight at weaning, for example, crosses exceeded inbreds by 28 pounds or 15 percent. These results compare favorably with published reports on crosses among lines less closely related than those studied here. The advantages shown by single-cross dams over inbred dams with respect to such traits as litter size or litter weight were equally as striking as the advantages shown by single-cross over inbred litters. In litter weight at weaning, for example, single-cross dams exceeded inbred dams producing inbred litters by 75 pounds or 36 percent.

Summary

In summary, the results suggest rather strongly that even though the selection practiced in the development of the Beltsville and Miles City lines did not appear to be sufficient to offset deleterious inbreeding effects, genetic differentiation among the lines due to differences in their genetic backgrounds, as well as differentiation resulting from the inbreeding practiced, definitely appeared to be large enough to result in cross combinations whose performance may well be considered to compare favorably with that of conventionally bred hogs.

DR. COCKERHAM: I have one question, if I may.

Do you think the superiority of the crosses over the purebreds is due to heterosis or due to selection among the pure breds in the inbreeding process?

DR. HETZER: Of course there was some selection in the inbreeding process but in spite of the selection factors there was some decline. Inasmuch as these purebreds were one of the parent stocks used in the production of these crosses, I would think that the difference would be more largely a reflection of heterosis than of individual differences, although we here at Beltsville do not have as critical a test of that inasmuch as these differences are comfounded with maternal effects, because we didn't have at Beltsville crosses out of purebred dams.

In Pennsylvania we did have crosses out of purebred dams and purebreds out of purebreds. On these farms in Pennsylvania, single-cross dams did considerably better than purebred dams on the same farm.

Does that answer your question?

DR. COCKERHAM: I think so.

DR. Kincaid: I might point out that the Miles City line referred to by Dr. Hetzer is still going there as a closed line and has been used in a reciprocal selection program with Yorkshires since 1954. It is still performing well for a line with as much inbreeding as it has.

DR. HETZER: I believe the title of my work said "Current Programs and Future Plans." We are not doing inbreeding now and I don't think we have any future plans for inbreeding in swine. We have other things that do seem to us a little more exciting now.

DR. WILSON: Dr. Hetzer, do your cross-bred dams produce better than your purebred Yorkshires?

DR. HETZER: I can't really answer your question because we didn't--

DR. WILSON: You said you recommend that farmers use a crossbred dam in a rotation program and I would be very skeptical that most crossbred dams would out-produce purebred Yorkshires.

DR. HETZER: The Yorkshires are very good in litter size--

DR. WILSON: I don't think I have ever seen consistent crossbreds out-produce a purebred Yorkshire.

DR. HETZER: I have heard the Hampshire people say that the Yorkshire was made for crossing with the Hampshire; otherwise the Yorkshire by itself would not stand up.

Of course, this is just second-hand information.

DR. KINCAID: Would this be crossbred dams that were crosses with the Yorkshire, too?

DR. WILSON: I would also stand on that.

DR. KINCAID: Do you think the Yorkshire, as a purebred, will exceed any cross with it?

DR. WILSON: It will do about as well, yes, and exceed most of them as far as these traits of reproduction are concerned.

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INBREEDING AND LINE CROSSING AS TOOLS IN ANIMAL IMPROVEMENT. RESUME OF COOPERATIVE STATE EXPERIMENT STATION AND INDUSTRY WORK IN SWINE. CURRENT PROGRAM AND FUTURE PLANS. 1/

C. E. Shelby, Director
Regional Swine Breeding Laboratory

INTRODUCTION

During the last century, purebreeding for the production of basic seedstock has become an almost world wide practice. Purebreeding results in a slow rate of inbreeding. Studies on the rate of inbreeding occurring in the formation and improvement of several breeds of livestock reveal that the average decrease in heterozygosity in each generation was about 0.5 percent. The breeding practices used in the Poland China breed during the period from 1889 to 1929 resulted in a Fx of 0.6 percent per generation interval of 2.5 years.

Inbreeding played an important part in the success of the swine breeders who laid the foundations of the various breeds. To a large extent, they fixed some desired characters by inbreeding using selected animals. Although inbreeding increased the ability of the animals to transmit their particular qualities to the offspring, it often lowered fertility, increased the rate of mortality in the pigs, and reduced size. Inbreeding fell into disfavor and was avoided by most breeders.

EARLY INBREEDING EXPERIMENTS WITH SWINE

Several experiments involving inbreeding pigs had been reported by 1930. The first of these in this country was started in 1908 at the Delaware Station, and continued for ten years. Projects were initiated later at the following stations: Iowa in 1921, California and the Bureau of Animal Industry in 1922, Oklahoma in 1923, Minnesota in 1924, and South Carolina in 1926.

All of the early trials were with small numbers. Mating plans were quite variable. The mating of close relatives was frequently practiced. Multiple mating was used. Selection was usually practiced. In general, the results were negative. Clemson College developed a successful show herd of inbred Berkshire from one boar and one sow.

1/ Presented at the Interbranch Genetics Council Symposium, held by the Animal Husbandry Research Division, April 14-15, 1965, at Beltsville, Maryland.

Only one line of pigs from the early trials is still in existence. The M line of Poland Chinas, started at the Waseca, Minnesota, station by Hodgson in 1924, is now at the Iowa station. The inbreeding is greater than 90 percent. Recently, nine of eleven blood antigen loci proved to be homozygous.

ESTABLISHMENT OF THE REGIONAL SWINE BREEDING LABORATORY

Animal breeders became increasingly aware in the early and mid thirties of the need for investigating the usefulness of different mating systems and methods of selection for improving performance characters in swine. The idea of organizing and conducting swine breeding research on a regional basis was advanced by early administrators. After some exploratory effort in 1936, a group of State and Federal research workers met to consider the implementation of a regional project in swine breeding. A plan was formulated, and approved by the North Central Experiment Station Directors and the Secretary of Agriculture in 1937. Federal funds were appropriated under the Bankhead-Jones Act.

The Regional Swine Breeding Laboratory was established in 1937 with headquarters at Ames, Iowa. Projects were organized and started at once. Research already in progress at Iowa, Minnesota and Oklahoma was revised and became a part of the regional program. Dr. W. A. Craft directed this cooperative research effort until his retirement in 1959. The original plan provided for organizing and conducting cooperative projects with the USDA at State Experiment Stations in the North Central States. Presently, active projects are located at ten of the 13 states signing the original Memorandum of Understanding, and North Carolina, which joined the Laboratory in 1963. Ohio will activate a project this year. Arkansas has cooperated unofficially with the group for many years.

The program was organized on a broad basis with all cooperating stations having similar objectives, but with each having wide latitude to investigate the problems in which it was most interested and best prepared to undertake. All research has been planned and coordinated through conferences of representatives of each of the cooperating states and the U. S. Department of Agriculture.

Information gained from their own experience over the past decade or more, and genetic experiments with plants and animals, including poultry, indicated to the project leaders that the most important problem to tackle was that of investigating as thoroughly as possible the consequences and uses of inbreeding and of crossing inbred lines. The spectacular success of hybrid corn was already apparent at this time.

OBJECTIVES OF THE RESEARCH

The objectives of the program as given in an early Annual Report were:

1. to discover, develop, and test procedures in breeding and selection which may be used by hog producers to speed the improvement of hogs with respect to performance including carcass characteristics.

2. to investigate precisely the usefulness of inbred lines for improving the breeding value of the pure breeds and for use in pork production.

3. to enlarge knowledge concerning the genetic effects of inbreeding and the inheritance of characters in swine, and

4. to evaluate and demonstrate application of such knowledge in swine breeding.

EARLY BREEDING PLANS

Initial breeding plans embraced the idea of forming inbred lines with selection based on performance. Earlier theoretical work led project leaders to believe that the depressing effects of inbreeding might be offset by selection with slow inbreeding allowing the production of inbred lines of high average merit. Lines from crossbred foundations were also planned with the ideas that: 1) such foundations offered opportunity for combining the best traits from two breeds; 2) opportunity for selection often is increased in early generations subsequent to crossing; 3) plant breeders had been successful in producing improved varieties from crosses.

METHOD OF SELECTION

Selection has been for single or multiple traits. Selection for multiple traits was based on either an index or a system of independent culling levels. Selection was usually for increased merit, but was for both high and low merit in one project.

Traits stressed included: 1) number of pigs farrowed, 2) number and weight of pigs weaned, 3) growth rate from weaning to 154 days in later years, to 180 days in early years, or on rate of gain from weaning to about 200 pounds, 4) efficiency of gain, 5) carcass desirability and 6) conformation.

EVALUATION OF PERFORMANCE

Methods of evaluation and composition of test groups differed importantly between stations. Systems of feeding varied to some extent. Samples of pigs from the various breeding groups were slaughtered at 200 to 225 pounds and carcass data collected. Although considerable variation existed in the production and carcass data collected, certain records were taken at all stations. These data have served to characterize the inbred lines, linecrosses, and control groups.

FORMATION AND DEVELOPMENT OF INBRED LINES

Foundation stocks of the inbred lines were obtained from many sources. Some stations used stock of known productivity already on hand. Otherwise, purebred stocks of differing pedigree origin were obtained from productive herds in various sections of the country.

Initially, 105 purebred lines were started. The distribution by breed was:

Duroc	35	Landrace	3
Poland China	34	Yorkshire	3
Chester White	24	Berkshire	1
Hampshire	5		

More recently, 10 Yorkshire lines were established and tested at one station and 20 at another. Too, eight lines from crossbred foundations were established. Three of these constitute new breeds.

Several methods of inbreeding were used. Some lines were inbred slowly with sufficient numbers to permit selection for performance. Other lines were inbred more rapidly. Single sows mated to a brother formed some lines.

Some lines were inbred by following definite plans of mating. In other lines, matings were based on performance with little attention to rate of inbreeding. In the latter, much freedom was available in making the matings each season within the line. A wide degree of closeness in mating resulted in such lines. Methods of inbreeding have differed at different stations and, even in different lines at the same station. Three different rates of inbreeding was tested in the formation of lines at one location.

Many lines were dropped after the first year or two because of low fertility or otherwise poor performance. Lines were culled both on performance of the lines themselves and of their performance in crosses with other lines.

Most of the stations have crossed two or more lines of the same breed at various times and started a new line from such crosses. Culling of lines was practiced more or less continuously in each of the projects.

Three views on the best method of forming lines exist: 1) that inbreeding should be at a low rate, using 15 or more sows and four or more boars per line of the same breed with selection against the undesirable traits uncovered by the inbreeding, 2) that inbreeding should be as rapid as possible using only three to six sows and one boar per line, or a single sow mated to her sire, son, or sib, discarding the poorest lines after two or three generations of inbreeding, 3) that a cross of two or more breeds be used as a base, proceeding to inbreed slowly, and selecting for the traits desired.

Combining the good traits of two different breeds in the development of lines from crossbred foundations was initiated by the USDA in 1935 using the Danish Landrace imported in 1934 and other breeds. Three of the lines formed by crossing the Landrace with other breeds are now recognized as new breeds, i.e., the Montana No. 1, the Maryland No. 1, and the Beltsville No. 1. The three Minnesota breeds were formed in the Laboratory. New breeds include:

1. Beltsville #1 - Landrace 74% and Poland China 26%.
2. Beltsville #2 - Danish Yorkshire 58%, Duroc 30%, Hampshire 6%, and Landrace 6%.
3. Lacombe - Landrace, Chester White, and Berkshire.
4. Maryland #1 - Landrace 63%, and Berkshire 37%.
5. Montana #1 - Landrace 58%, and Hampshire 42%.
6. Minnesota #1 - Tamworth 52%, and Landrace 48%.
7. Minnesota #2 - Inbred Poland China 60%, and Canadian Yorkshire 40%.
8. Minnesota #3 - Welch, Large White, Glouchester, Old Spot, Beltsville #2, Minnesota #1, Minnesota #2, Poland China, and San Pierre.
9. Palouse - Landrace 53%, (65) and Chester White 47%, (35).
10. San Pierre - Berkshire, and Chester White.

Performance in the new breeds has been good in many respects. Each has shown some merit in crossing to produce market hogs. Meat type can be improved in most lines. The Inbred Livestock Registry Association, Augusta, Illinois, registers animals in the new breeds. Total numbers are small compared with conventional breeds.

The steps followed in the formation of the Minnesota breeds were:

1. breeds chosen possessed the characteristics desired, but were widely divergent genetically.

2. foundation animals of high individual excellence and/or with a background of performance were chosen

3. breeding was within a closed herd

4. rigorous selection was practiced from the outset for factors affecting economy of production.

CONSEQUENCES OF INBREEDING

The effects of inbreeding have varied among the different lines. In general, the number of pigs born and raised and growth rate tended to decline appreciably with inbreeding. Conversely, these same traits exhibited the most heterosis in crosses. Litter size was much more difficult to maintain in lines being inbred, than was growth rate. The incidence of stillborn pigs increased slightly with inbreeding of the dam. Carcass desirability and economy of gain were little affected by inbreeding.

The decline in number of pigs farrowed for each increase of ten percent in inbreeding was estimated from pooled data to be about one-third of a pig per litter and in number weaned about one-half pig. Strength and liveliness of pigs at birth was reduced in some lines with increased inbreeding. Rate of growth declined in some lines, but apparently not in all. Economy of gain improved slightly in some lines.

Differences in performance between lines usually became evident by the time inbreeding had reached 25 to 35 percent.

Although inbreeding adversely affects pre-weaning performance characters, the over-all results indicated that when selection was practiced to the fullest extent possible, some lines would perform reasonably well, at least, for several generations of inbreeding at a moderate rate.

Lines formed from breed crosses may have been slightly less sensitive to the depressing effects of inbreeding than lines from the pure breeds.

Physiologic Changes

The rate of physiologic maturity declined in some lines. Age at first heat in gilts and at first service in boars increased as inbreeding progressed in the line. Inbred gilts shed less ova than non-inbred gilts. Fewer eggs were shed each heat period in certain lines. The development of the testes and production of sperm in the boar were delayed by inbreeding. Lines differ in rate of testes growth and development, substances secreted, sexual behavior and age at first service. Highly inbred boars from some lines were lacking in libido. Too, highly inbred gilts from some lines were difficult to settle. Gestation periods for sows seemed to have lengthened a little by inbreeding.

Incidence of Genetic Defects

Many types of abnormalities occurred in the pigs of the various populations in the cooperative projects. Their actual incidence was much less than was expected by many workers. Relatively few inbred lines were discarded because of specific defects. Included among the defects were cryptorchidism, hernia, atresi ani, hemophilia, cleft palate, and blindness.

LINECROSSES

The principal value of inbred lines is due largely to whatever advantages are obtained from their use in crosses. Trials for testing them in various types of crosses were conducted by each of the stations.

Generally, the lines tested were those performing best as lines, but some were definitely inferior in one or more respects. Performance of the lines themselves was not a good indicator of their crossing value with each other or with noninbred stock.

Trials have included crosses of lines belonging to the same breed and to different breeds. The characters most adversely affected by inbreeding show the most favorable response to crossing.

Both two-and three-line crosses were made. Most comparisons were with parent lines, but a few were with non-inbred stocks.

Two-line crosses have excelled parent lines in number of pigs farrowed and weaned and growth rate to weaning. Three-line crosses generally exceeded two-line crosses in pigs farrowed and weaned.

Maternal ability of linecross sows is definitely superior to the parental lines and generally to non inbreds. Growth rate of pigs from linecross sows reflects the hybrid vigor of the dams up to weaning, but differs little later from two-line cross pigs.

Linecrosses show less advantage when compared to noninbreds. Only three-line crosses have shown advantages over the controls in numbers of pigs. Two- and three-line crosses have shown a slight advantage in individual pig weight at six months. On a litter basis, the three-line crosses excel noninbreds by about 15 percent at six months.

Linecrosses of different breeds have produced more "hybrid vigor" than crosses of the same breed. Best results within a breed were obtained when the lines used had the least relationship.

TOPCROSSES

Inbred boars of several different lines were compared with noninbred boars in topcrosses on similar groups of sows on cooperating farms in Wisconsin. In about half of the lines tried, pigs by inbred boars showed a definite advantage in rate of gain over pigs by noninbred boars. Performance of gilts from litters by inbred boars excelled that of gilts by noninbred boars by about one pig per litter at farrowing and weaning and about 37 pounds in weaning weight of litter.

Inbred boars of different lines were used in rotation to produce "rotation linecrosses". Some advantage was evident in favor of the between breed over the within breed rotation linecrosses.

Genetic diversity of the lines appears important to heterosis in crosses. Crossing trials have generally emphasized the importance of combining ability in swine.

SELECTION ATTAINED

Selection was practiced for maternal ability, vitality, growth rate, conformation, economy of gain, and carcass desirability. Use of the latter two criteria has varied greatly between stations due to varying circumstances. Losses due to disease imposed limitations on selection at most stations at one time or another.

An extensive report relating to selection practiced in seven projects revealed that selection differentials were positive, but small. Not all the opportunity for selection was exercised. Response to selection was less than expected on the basis of the heritability estimates and selection differentials.

Average selection differentials obtained from six stations are indicated below:

Number born + 0.34 pigs	Indiv. 154 day wt. + 14.9 lbs.
Number weaned + 0.65 pigs	Index + 27.4 points
Litter wean. wt. + 22.3 lbs.	Fx of dam - 1.48
Indiv. wean. wt. + 3.64 lbs.	Fx of indiv. - 1.13

Most of the selection for size of litters was automatic, merely because of the availability of more pigs from which to choose breeding stock in the larger litters.

A consistent tendency to select animals from the less highly inbred litters was noted. Selection for the least inbred animals was assumed to be an indirect result of selection for superior performance both of litters and individual pigs.

ESTIMATES OF HERITABILITY

Numerous estimates of heritability were obtained from the inbreeding experiments. Presently, the following values seem realistic:

Production traits	Carcass traits
Number farrowed - .10	Area of loin eye - .50
Number weaned - .10	Thickness of backfat - .50
56 day litter weight - .10	Length - .60
5-month weight - .30	% ham and loin - .40
Efficiency of gain - .30	Conformation Score - .25

CARCASS INVESTIGATIONS

Samples of various inbred lines and linecrosses were slaughtered and carcasses evaluated at most stations. Certain carcass traits, like fatness, differed importantly between breeds and between lines within the same breed. Carcasses from linecrosses of divergent lines have been intermediate for the individual traits.

Usually, linecross carcasses were superior to either of the parent lines due to a combination of desirable traits. Crossbred carcasses were usually superior to linecrosses.

Studies of carcass data indicated clearly that important genetic differences exist between lines. The heritability of several important carcass traits is known to be 0.50 or greater. Over-all results confirmed that selected inbred lines may be crossed to produce the type of carcass desired without sacrificing growth rate or economy of gain.

RECENT STUDIES

Two projects investigating the use of rapid inbreeding with selection in evaluating and utilizing potential sources of superior germ plasm were terminated in 1964. Twenty Yorkshire lines were tested on one station and ten at another. Productive stocks were obtained from divergent sources.

In the Michigan project, lines were formed from single females mated to a full brother or son. Noninbred litters were subsequently produced by breeding the sow to sons, grandsons, and great grandsons. Many lines were lost in development. The losses were probably a positive type of selection against undesirable genetic material. This method of sampling new lines was relatively efficient.

The major findings of this project were:

1. productive ability decreases with inbreeding, but is restored when lines are crossed.

2. most of the response of crossing lines appears to be general rather than specific combining ability.

3. the effect of crossing is very marked on the mothering ability of the female.

4. there is no marked increase in phenotypic uniformity within the lines or in the crossline litters.

Dr. Magee (1963) concludes, "Therefore the development of highly inbred lines and testing them in crosses to develop specific highly productive crosses should not be undertaken until less complex and expensive breeding plans have ceased to give fruitful results."

COMMERCIAL USAGE

During recent years, production and sale of "hybrid" boars have become an important business. Several companies now specialize in producing boars bred to cross well with available female stock. Approximately 7,000 hybrid boars are marketed annually by the five largest companies. To date, this practice has not been impartially evaluated.

In the largest operation, five major lines (breed synthetics) are necessary to provide adequate crosses. Hybrid sale boars are produced by rotating sires from three or more related lines on females in producer's herds. Superior germ plasm is bought in the industry whenever and wherever obtainable and injected into the individual lines after preliminary testing. One or two generations of close mating is used to insure greater prepotency and to purge the stock of genetic defects. Meatiness is very good.

Another company maintains seven new breeds developed from crossbred foundations. Approximately half of the boars marketed are purebreds and half are hybrids (rotation or first crosses). No doubt some inbreeding results from the small size of the individual lines and the limited sources of new germ plasm. The amount of intentional inbreeding is unknown.

THE FUTURE OF INBREEDING

Recently, the last inbreeding project was terminated. With the end of this era in swine breeding research, the reasons for its passing should be examined. These include:

1. The techniques used by the hybrid corn breeder were not readily adaptable to swine. The length of time and costs to produce and test lines adequately both as lines and in crossline combinations was excessive. Relatively few lines could be sampled and tested. Sales income was low.

2. Intense selection with mild inbreeding did not produce a remarkably superior animal. Results of crossline matings were not exceptionally promising. The individuals sampled probably were not from the best available stocks.

3. The degenerative changes due to inbreeding resulted in many practical problems in the production and maintenance of highly inbred stocks for commercial usage.

These trials have not proved conclusively that inbreeding techniques are not usable in swine improvement. Until genetic theory has been further clarified or much more efficient and simpler methods of evaluation and maintenance developed, it is doubtful if its use is economically feasible even in large commercial operations.

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SUMMARY

Although inbreeding had been or was being studied by a few agricultural experiment stations at the time of the establishment of the Regional Swine Breeding Laboratory in 1937, this cooperative research effort was the first major step in systematically investigating the consequences and use of inbreeding.

The development and testing of inbred lines as individuals and in crosses was emphasized during the first 15 to 20 years of work in the Laboratory. Approximately 140 inbred lines within seven major breeds and eight crossbred foundations were started. Most of these were discarded because of poor performance or lost in early development. A few reasonably good lines were developed. More recently, the change from lard to meat type has made the surviving lines obsolete and of little economic value.

Selection criteria included sow productivity, vitality, growth rate, economy of gain, conformation, and carcass desirability.

Lines become differentiated genetically for performance characters when inbred 25 to 35 percent. Litter size and vitality deteriorated importantly with inbreeding. Growth rate declined to a lesser extent. Economy of gain and carcass traits were little affected.

Certain reproductive problems resulted with inbreeding. Sexual maturity was delayed in both boars and gilts. Boars were less fertile. Gilts were difficult to settle. Highly inbred boars lacked libido. A slightly greater incidence of genetic defects occurred.

Fertility, liveability, and growth rate were restored in line crosses, equaling or exceeding parental lines. Maternal ability of linecross sows often exceeded noninbreds. The lines most divergent genetically yielded the most hybrid vigor in crosses. Crosses of lines from different breeds have generally shown higher levels of performance than crosses belonging to the same breed.

Selection was practiced concurrently with inbreeding. Differentials attained were low, but positive. Response to selection was considerably less than expected. Selection did not produce a superior line or breed. Present estimates of the heritability of maternal ability, individual growth rate, and carcass traits are about .10, .30, and .50, respectively.

Definite differences exist between lines in carcass characteristics. Some inbred lines consistantly yield excellent carcasses, while others yield excessively fat carcasses. Carcasses from line crosses were generally intermediate between the parent lines for the individual traits.

Although inbred lines and linecrosses have shown some advantage in swine improvement, their use is not recommended until less complex and costly plans have ceased to give fruitful results.

ACKNOWLEDGMENT

Much of the basic material presented here was taken directly or adapted from the reviews by Dr. Craft. Extensive bibliographies are given in the papers listed below. My own opinions are also included.

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INBREEDING AND LINE CROSSING IN POULTRY

S. P. WILSON

Early reports of the effect of inbreeding on various traits of the fowl (Dunn 1923, 1928; Hays 1924, 1934; Goodale 1927; Jull 1929a, 1929b, 1933; Waters 1941, 1945a, 1945b, 1945c) substantiate the general principle that inbreeding nearly always has a depressing effect. However, it may or may not act in a progressive or cumulative fashion as inbreeding continues. The magnitude of depression associated with given levels of inbreeding is primarily determined by the genetic mechanism of the trait, with the least affected traits being those showing a high degree of additivity. Most of the earlier reports were severely limited in that there was a lack of specific information either on the intensity of inbreeding or selection practiced.

Shoffner (1948) presented evidence that hatchability and egg production are seriously affected (an extrapolated drop of approximately 60% when inbreeding reaches unity) while sexual maturity is affected less severely (an increase in age at sexual maturity of 30%), and body weight and egg weight hardly at all. These results are shown in Table 1.

TABLE 1. Regressions, mean performance, and the relative change expected if there were 100% inbreeding.

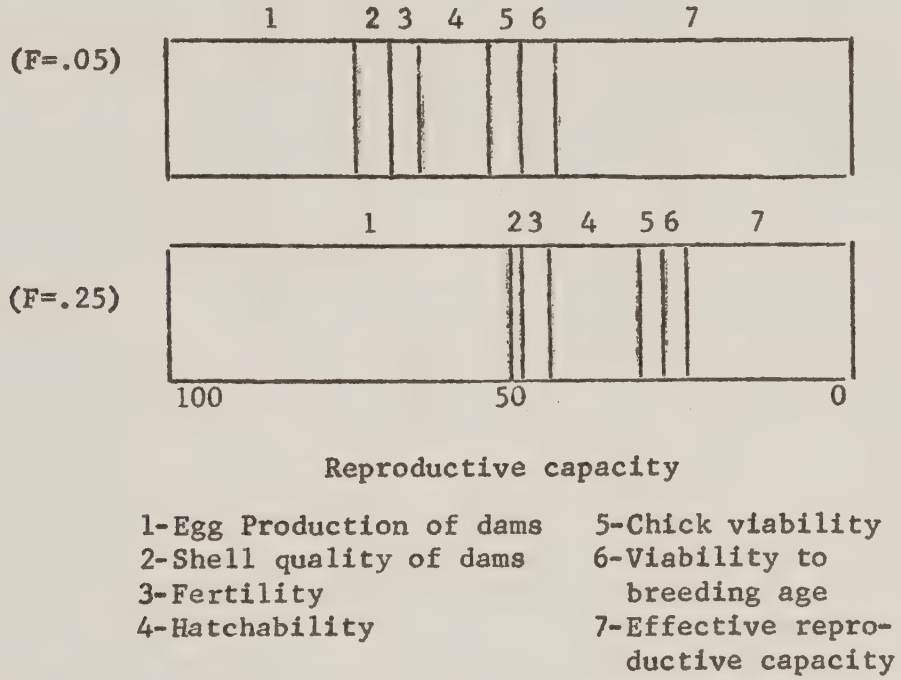
	b	Mean Performance	Relative Change (%)
Hatchability	-.436	68.26 %	-63.9
Egg production	-.926	148.52 eggs	-62.4
Sexual maturity	.597	202.66 days	29.5
Body weight	-.004*	4.75 lbs.	-8.4
Egg weight	-.002*	24.50 oz.	-.8

*non-significant

Lerner (1958) (Figure 1) diagramed the results of an analysis by Düzgünes (1950) of the causes of reduction from the potentially possible fitness of a production-bred flock of chickens (F=0.05) and of mildly inbred lines extracted from it (F=0.25). The reproductive capacity on the horizontal scale refers to the relative proportion of offspring per dam surviving to nine months of age. The length of the hatching season was kept constant (28 days) so that each dam had a potential reproductive capacity of 28 offspring, equivalent to 100%. If only 14 birds were alive at nine months of age, relative fitness would be 50%. The first six blocks indicate the proportionate

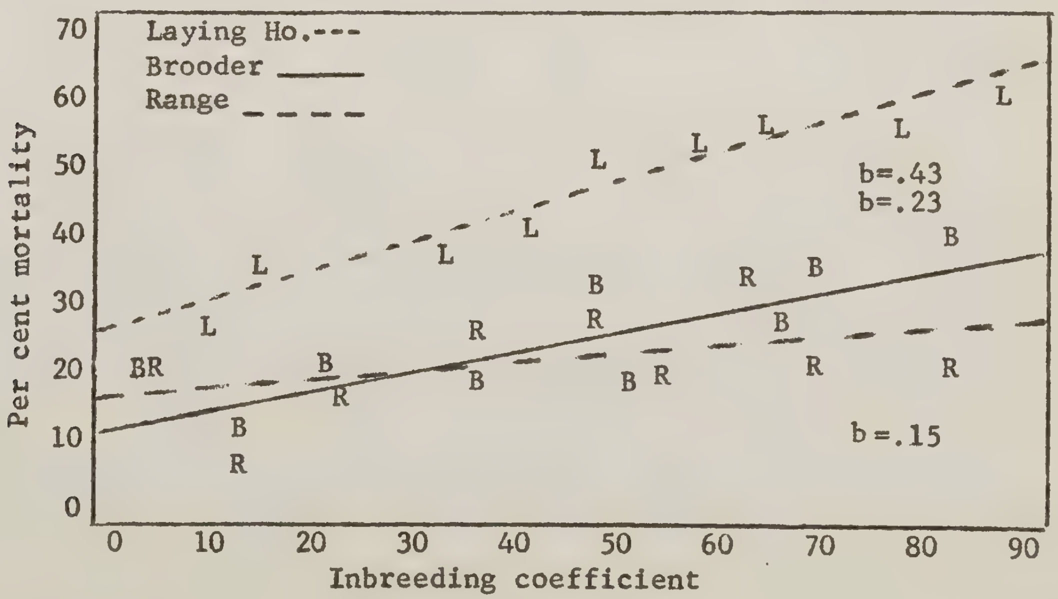
reduction from the maximum at different stages of the reproductive cycle. Block 7 shows the proportion of offspring alive at nine months of age.

FIGURE 1. Effect of inbreeding on reproductive fitness of the chicken.



It may be seen that an increase in inbreeding from 0.05 to 0.25 reduced fitness by more than one-half. In this illustration, most of the components of fitness, particularly the fecundity of the dams and the hatchability of the embryos, show a decline. In this study, viability from time of hatch to breeding age appears to be independent of the degree of inbreeding whereas in Figure 2, taken from data by McLaury and Nordskog (1956), a positive regression of mortality rate on inbreeding can be observed.

FIGURE 2. Effect of inbreeding on viability of the chicken



The results of a study by Blow and Glazener (1953) are shown in Table 2. Their results were in rather close agreement with Shoffner's in that body weight and egg weight were little affected by inbreeding, whereas sexual maturity, egg production and hatchability were rather seriously affected in a detrimental manner.

TABLE 2. Effect of inbreeding on traits of the fowl.

Character	Mean performance for 1946	Regression on inbreeding	Expected change with 100% F
Body weight	2,111 grams	$-1.044 \pm .851$	-104 grams
Egg weight	58 grams	$-.018 \pm .021$	-1.8 grams
Sexual maturity	194 days	$.315 \pm .013$*	+ 31 days
Egg production	117 eggs	$-.302 \pm .112$*	- 30 eggs
Hatchability	69 %	$-.371 \pm .111$*	- 37 %

*P=.05

Warren (1942) reported results of five specific breed crosses with six traits measured. Of these 30 comparisons, in six the crossbreds were better than either parent; in five one cross was superior to either parent and the reciprocal like the better parent; ten were like the better parent, and nine were like the poorer parent. Thus in 21 of 30 comparisons the crossbreds were equal to or better than the superior of the two stocks.

Table 3 presents the results of a two year experiment by Knox (1950) in which the progeny of the mating of inbred Rhode Island Red males

TABLE 3. Average first year egg production of progeny in relation to kinds of matings.

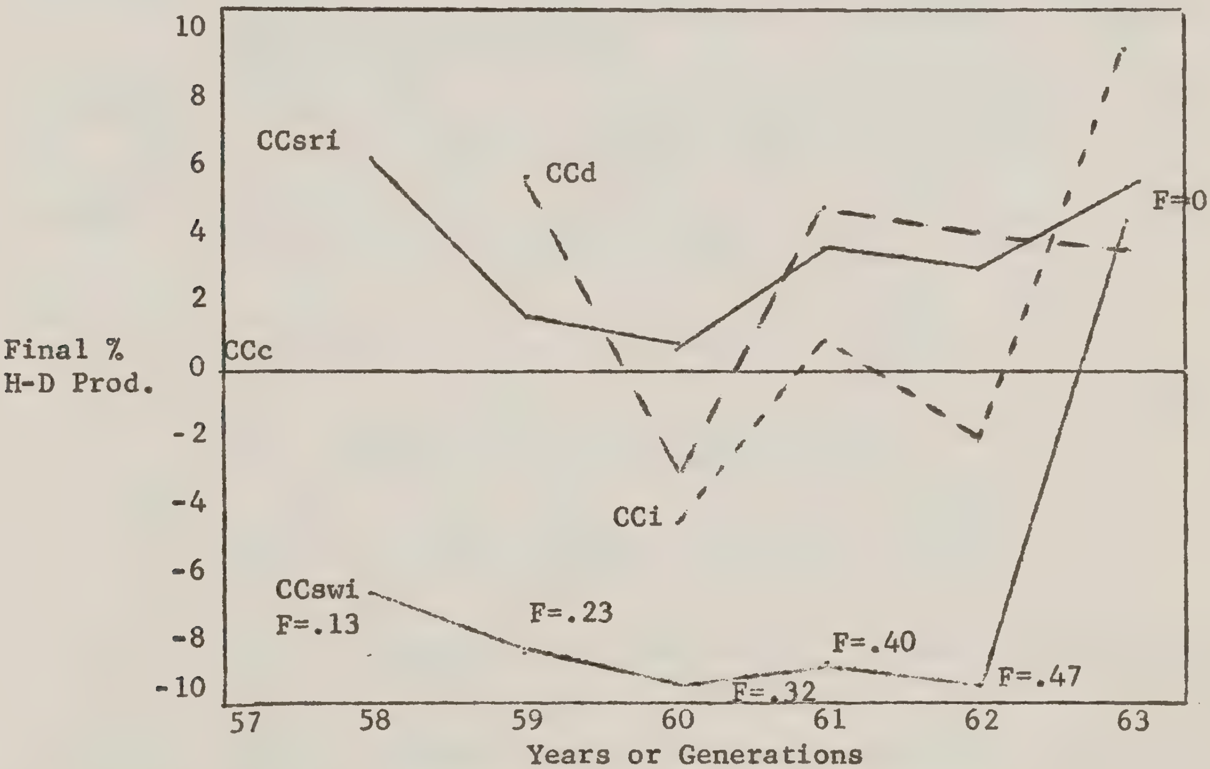
Mating	Mating type	Production 1946-47	1947-48
1	O.B. R.I.R. ♂ x O.B. R.I.R. ♀	219	199
2	O.B. R.I.R. ♂ x O.B. W.L. ♀	229	208
3	I.B. R.I.R. ♂ x I.B. W.L. ♀	239	230
4	O.B. W.L. ♂ x O.B. R.I.R. ♀	250	240
5	I.B. W.L. ♂ x I.B. R.I.R. ♀	255	240
6	O.B. W.L. ♂ x O.B. W.L. ♀	221	182

and inbred White Leghorn females produced at a higher rate than progeny of outbred Rhode Island Red males and outbred White Leghorn females. However, the progeny of inbred White Leghorn males and inbred Rhode Island Red females did not outproduce the progeny of outbred White Leghorn males and outbred Rhode Island Red females.

Preliminary results of work in progress at the North Central Regional Poultry Breeding Laboratory at Lafayette, Indiana are shown in Figure 3 as deviations from control line (CCc). Population CCswi is composed of five inbred lines with four sires per line and 25% selection, based on sire family averages, practiced in each line. CCsri is propagated by the best five of 20 sire families being selected and mated in such

a way as to restrict inbreeding. In each of these populations the 20 sire families are evaluated by the production of 60 daughters per sire. Population CCd is selected on dam family averages where 125 dams are evaluated on the production of 5$\pm$ 1 daughters each. The best 25% of these families are saved and mated randomly to males from the selected families. In population CCi selection is based on individual production. Selection pressure on the females is 12.5% and the males are selected at random, thus giving an overall selection pressure of 25%.

FIGURE 3. The effect of various selection systems and crossing of inbred lines on egg production.



The most interesting development in this study occured when the five inbred lines of CCswi were crossed in the 1963 test. Production of the crosses was almost identical to the CCsri where selection pressure was the same but inbreeding had been restricted. In each case production was somewhat better than that of the control.

SUMMARY

It is quite evident that inbreeding exerts a detrimental effect on most traits of the fowl, varying in degree of severity with the type of genetic mechanism controlling the trait. It is also clear that crossbreeding and crossing of inbred lines generally produces a favorable action known as heterosis. However, the genetic mechanisms of heterosis are not clear and are as yet unproven; also, the precise inter-relationships between intensity of inbreeding and degree of resulting heterosis are not known. There are also divergent views on the question of whether a maximum degree of heterosis is obtained from crosses of common or divergent origin. Another important question is concerned with the breeding techniques needed to ensure continuous improvement of crosses rather than standstill performance which in many cases has occured. Answers to any or all of these problems would certainly be beneficial in the utilization of heterosis for the production of farm animals.

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PROBLEMS AND PROGRESS IN INBREEDING CHICKENS

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Introduction:

The inbred lines of White Leghorns maintained at the Laboratory were initiated in 1939 by Dr. Nelson F. Waters. They were established for use as experimental material in the study of the avian leukosis complex, and not as foundation stock for the study of other economic traits. In the early years the lines were selected either for resistance or susceptibility to this disease as it occurred naturally on the Laboratory premises. During this period inbreeding proceeded at a rate consistent with the maintenance of reproductive ability and sublines were occasionally crossed. Under this system all lines had reached an inbreeding coefficient of at least 95% by the twentieth generation.

Progress of Inbreeding:

Since these lines had been developed for research in a disease where uniform response to experimental treatment was desirable and transplantation studies could contribute fundamental knowledge, it was decided to evaluate the progress of inbreeding experimentally. One method often used is the exchange of skin grafts. This was done in adult birds in several of the lines. Data on three lines are presented in table 1. None of the lines have reached the stage of complete histocompatibility, but more than 50% of the grafts exchanged within line 7 survived more than 100 days. Another measure of homozygosity is the number of alleles segregating at the blood group loci. In cooperative work with Dr. Warren Johnson of

Auburn University the tentative number of alleles at eight loci have been identified. Table 2 presents this data. This is probably an over estimate of the amount of segregation presently in the lines because it includes all the loci identified since this study started in 1958. Some of the lines are segregating at two loci involved in specific cellular resistance to the growth of avian leukosis viruses, and a hemoglobin polymorphism has been noted in one. Therefore, considerable detectable genetic variation remains.

Currently we are full-sib mating within lines with about nine sires per line. We have adopted this procedure because we feel that highly inbred experimental animals are desirable for our work. We are evaluating variation in reproductive ability among families within lines prior to adopting a system of selecting among sablines. Table 3 gives the results of analyses of variance of percent production and percent hatchability of fertile eggs. Considerable variation among families is evident and reproductive ability has not declined. We feel that we will be able to produce reasonably productive full-sib mated lines from this source.

Results of Crossing:

Several diallel cross experiments have been conducted with three of these lines, for the purpose of studying responses to natural and artificial exposure to avian tumor viruses. Limited observations have been made on other traits. Table 4 gives the effect of crossing on the hatchability of fertile eggs and the livability of chicks to 30 days of age. There is an obvious benefit of crossing in both of these traits. In contrast there has not been an increase in resistance to leukosis on crossing. In fact in some specific cases

the crosses have been much more susceptible than the pure lines. The fact that two loci with dominant genes for susceptibility have been identified precludes a general benefit of crossing on resistance to this disease.

<u>Summary</u>:

Limited data on long term inbreeding in chickens have been presented, and it is suggested that with careful selection among families full-sib mated lines can be maintained. Crossing appears to favor early survival but has no general benefit on specific resistance to leukosis.

Table 1

Number of skin grafts surviving 100 days after exchanges among adult chickens within three inbred lines

Line	No. Grafts	No. Survived	Percent Survival
7	159	91	57.2
9	160	0	0.0
15I	89	9	15.2

Table 2

Segregation at 8 blood group loci in RPRL inbred lines

Line	Number of genes in system							
	A	*B*	*C*	*D*	*E*	*I*	*P*	*Q*
6	2	2	1	1	2	1	1	?
7	2	1?	2	1	2	2	1	2
9	2	2	2	2	3	2	2	2
15	1	3	2	2	2	2	2	1
15I	1	3	2	2	2	2	2	1

Table 3

Analysis of variance among full-sib mated families for percent production and percent hatchability

Line	Year	% Prod.	Sign.	% Hatch	Sign.
6	62-63	47.4	NS	4619	**
	63-64	38.7	NS	65.2	*
	Pooled		NS		**
7	62-63	47.4	NS	70.9	NS
	63-64	35.1	**	71.1	NS
	Pooled		**		NS
9	62-63	41.0	**	71.7	*
	63-64	30.3	NS	72.0	*
	Pooled		**		**
15	62-63	44.6	NS	67.0	NS
	63-64	37.4	**	69.3	NS
	Pooled		**		*

Table 4

Percent hatchability and percent chick livability to 30 days in a 3 x 3 diallel cross experiment

Female Parent	Male Parent: 6	7	15I
6	70.8 / 83.5	84.3 / 96.0	84.4 / 96.7
7	80.1 / 92.0	66.1 / 73.8	79.0 / 91.6
15I	75.3 / 86.2	81.4 / 87.9	58.8 / 77.9

Upper number = Percent hatchability
Lower number = Percent livability

DR. COMSTOCK: I missed what you had to say because I came in late about how highly inbred they were.

DR. CRITTENDEN: About 1958 was the last time that inbreeding coefficients were calculated and I haven't gone back to all of Waters' calculations but he stated they were in excess of 95 per cent. I am worried some about this because at that time he had some different sub-lines and the individual birds could have a high inbreeding coefficient.

DR. COMSTOCK: That would be my next question, whether the lines were broken into sub-lines?

DR. CRITTENDEN: Yes, there were some sub-lines and are some now.

DR. COMSTOCK: There was a time when some of the mice people were talking about segregation in having inbred lines in mice and I read a paper where they investigated one of the lines and they said it was probably just genetic differences between sub-lines.

DR. CRITTENDEN: Yes. I would like to work with Warren Johnson some more and see what has happened to the blood group loci in these three generations of full-sib mating.

DR. KYLE: On that last one, were both of those resistant and the cross susceptible?

DR. CRITTENDEN: At least to that dose of virus. Line 6 is resistant to lymphomatosis, and it is apparently a host-reaction type of thing rather than some of the cellular resistance I mentioned earlier. But at least to the lymphomatosis form of the disease, Line 6 is quite resistant and Line 7 is quite resistant to the virus in cell culture, so the virus doesn't grow in Line 7 where as it apparently does in Line 6. There may be some explanation of this increase on the basis of the cross.

COMMERCIAL APPLICATION OF INBREEDING AND INCROSSING IN THE POULTRY INDUSTRY*

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Inbreeding programs for the purpose of developing superior laying strains of poultry have been developed chiefly as a result of the phenomenal gains made in the production of hybrid corn. Another factor contributing to the development of inbreeding schemes has been the difficulty that numerous poultry breeders have experienced in further increasing the level of egg production over that attained by the progeny-testing methods of selection and breeding carried on for several years without inbreeding.

The poultry breeding industry has changed rapidly during the past two decades from the small local breeder, using progeny testing methods, and serving a relatively small local area to the large commercial poultry breeding enterprise operating on a regional, national or in many cases, international basis. These large commercial breeders have developed well staffed research departments, extensive testing facilities and distribute their final product to the poultryman through a series of so-called associate or franchised hatcheries. The associate hatcheries generally serve as multipliers for the breeders by maintaining the parent stock for producing the commercial chicks.

The poultry breeders of pre-World War II or of the postwar period developed lines of excellent genetic background that would fit into many of the commercial operations today as strains or as

*Talk at Inter-Branch Genetics Council Meeting, April 14-15, 1965.

lines for inbreeding. In fact, many of the stocks were probably inadvertently inbred to a considerable extent. Many of the smaller breeders regularly followed the practice of line breeding to incorporate the desirable traits of selected individuals into their stocks.

The practice of inbreeding and subsequent crossing in todays poultry breeding operations is largely confined to the egg strains. Egg production is generally considered to be a trait of rather low heritability (.10 - .15) whereas growth rate or body weight at a given age has a moderate to high heritability (.40). Most of our commercial broilers or turkeys are produced by breed or strain crossing, with specific lines selected for their role as male or female parents.

Inbreeding as such has two main purposes in the production of superior laying stocks. The first purpose of inbreeding is to develop strains of birds relatively homozygous for genes determining high egg production. When close inbreeding is followed, frequently undesirable genes are also revealed. Rigid selection of the inbreds must be practiced each generation to eliminate the undesirable genes and reduce variability in the lines. Secondly, inbreeding is practiced to develop lines of a breed or variety for the purpose of crossing with other inbred lines of another breed or variety.

<u>Use of Inbreeding and Incrossing</u>

Today, the majority of the 335,000,000 commercial layers used in the United States are produced by a few large commercial breeders.

In fact, we could probably safely estimate that 95% of all laying hens used commercially are produced by fewer than 12 commercial breeding companies. It is very difficult to obtain accurate information on the extent of inbreeding practiced by the breeders. However, it is well known that three of the major breeders are merchandising a laying bird developed following an inbreeding and incrossing system. In most all cases, the commercial bird is the product of a four-way cross.

The degree of inbreeding used to develop the inbred lines remains a trade secret with the individual breeder. The most usual procedure following the selection of a strain with a desired characteristic or characteristics is to start inbreeding following either a full brother-sister or half brother-sister matings. Testing programs are started simultaneously with the inbreeding program to determine the combining ability or "nicking" ability with other lines. Most commercial breeders have extensive testing programs in operation at all times, constantly searching for lines that will combine well to impart the desired traits to the final product, the commercial layer. Thus, a four-way cross may contain lines with different degress of inbreeding. Also, we can only speculate as to the coefficient of inbreeding in the selected lines. One major breeder recently reported that one of his best lines had been intact for over 20 generations. With full brother-sister matings this line would be approaching the 100% inbred mark or with half brother-sister matings the line would be expected to be above 50% inbred. Regardless of

the degree of inbreeding of this particular line, the commercial product marketed by this breeder probably contains other lines with little inbreeding.

The Federal Trade Commission issues rules covering advertizing. A few years ago this regulatory agency outlined the definition of a hybrid chicken. In effect, the ruling stated that for a bird to be advertized as a hybrid it must have been produced from parent lines having an inbreeding coefficient of at least 37.5% or the equivalent of 2 generations of full brother-sister matings. We have not seen a chicken advertized as a "hybrid" since the date of the ruling. Today, chickens produced from the crosses of inbred lines are referred to as incrosses. One major breeder reports in advertizing that a good inbred generally results from five generations of full brother-sister mating.

We could probably safely say that the degree of inbreeding practiced by poultry breeders is very low as compared to the corn breeders. Also, it is very doubtful that extensive inbreeding is practiced by any animal breeders for the production of incrosses. The detrimental effects of intensive inbreeding have been amply documented in the literature.

The popularity of inbreeding and incrossing in poultry can be demonstrated by looking at the numbers of breeders tested as a part of the National Poultry Improvement Plan. It is estimated that the breeding birds in the Plan (NPIP) represent approximately 70% of the total, which should be an adequate sample to estimate breed distri-

bution information. The distribution of birds by breed and crossing system are presented in Table 1.

Table 1. Breed and Cross Distribution in NPIP Hatchery Supply Flocks*

Breed or Cross	Year		
	1944-45	1953-54	1963-64
	%	%	%
New Hampshire	20.6	25.4	.6
White Leghorn	25.8	18.9	11.8
White Rock	17.5	23.1	6.1
Barred Rock	12.4	2.2	.3
Rhode Island Red	8.0	2.7	.6
Cross Mated	9.8	19.7	73.5
Incrossmated	---	5.1	6.5
Other	5.9	2.9	.6
Total (No.)	17,573,321	36,027,365	35,759,267

*(From ARS 44-2 revised November 1964)

The values presented in the table are summarized for all participating states and include both egg and meat type chickens. According to the Statistical Reporting Service, approximately 25% of all chickens produced each year are egg type. The remaining 75% would represent broiler or meat type chickens. The total breeding flocks, including both meat and egg stocks, include about 6.5% incrosses which can be assumed to be egg type.

A similar breakdown of the egg producing stocks will give us an estimate of the total egg producing stocks that are incrossbreds. The values for 1961-62 are shown in table 2.

Table 2. Distribution of Egg Producing Stocks by Breeds and Crosses

Breed or Cross	Year 1961-62 %	Total by Classes %
White Leghorn	57.6	
Rhode Island Red	3.8	61.4
Incrossmated	27.1	27.1
Calif. Grey x White Leghorn	4.6	
RIR x Barred Rock	4.3	
Crosses of egg stocks (3 or 4-way)	2.6	11.5

From these values which represent approximately 70% of the total, we can see that 27.1 percent or approximately 90 million commercial chicks are produced from incrossbred matings. These values include the strain crosses as purebreds. Thus, the White Leghorns would be expected to be largely strain crosses within the White Leghorn breed.

Incrossing vs. other breeding systems

During the past ten years incrossing has been practiced by a number of poultry breeders. However, when compared to strain crossing, it is evident that the latter system has been gaining in popularity. The breeders using strain crossing expect to obtain the majority of the advantages of heterosis by selecting individual strains that combine well or have "nicking" ability, without all the expense of developing inbred lines.

DR. BAYLEY: Are there any questions for Dr. Cook before we proceed?

DR. KING: Where did you get 135 million as the number of egg layers? I have a feeling that is closer to 300 million.

DR. COOK: These came from the latest Argicultural statistics. We have over 300 million hens and pullets, but in dividing them there are probably 135 million mature hens. I think by definition the Agricultural statistics would classify anything as a pullet until it reached 12 months of age. This means you have at least six months of production coming from those birds that would be classified as pullets. So from a realistic viewpoint, there would be nearer 300 million.

DR. CRITTENDON: They told me they sold about 130 million chicks last year.

DR. COOK: This we can compute readily by looking at the information we have available, but it is interesting to me that many of our commercial breeders now are booking chicks on the basis of 90 per cent or better eggs set, so they are getting real good hatchability.

DR. WARWICK: I assume this information is available and you might be in a position to just make a general comment on it.

Do these incrossmated birds in general perform better or poorer for the various criteria than the others? Is the production of them growing? Do you anticipate it will grow or go down or what?

DR. COOK: I will try to recall some of those figures.

With regard to your first question, if we look at the results from the random sample tests, I don't think we can say they perform better than the birds from the strain-crossed systems. If you want to pick out the higher producing lines you will find strain-crossed birds will rate up just as well as the ones from the incrossed system. I am looking at the breakdown of the various data by years. In looking at the data we find that in '53- '54 the number of incross breeds was quite low. They came up quite rapidly. They went up to about 7 or 7-1/2 per cent; in the last year or two they have been fluctuating. I don't think there are enough years to give you any trend but in general this is what has happened in the last 15 years.

DR. COMSTOCK: I have an impression and I want to check it with you in terms of what you say.

I have the impression that the system of selection, or the system of breeding that the incrossers, as you define them, use, and strain-crossers use, is different in degree only. In other words, I have the impression that in both instances they are selecting for combining ability, selecting within populations, whether it is within these so-called inbred lines that they don't want to say are inbred more than 37-1/2 per cent or whether it is within a larger and less inbred population.

DR. COOK: I think you are correct. This is the same impression that I have and I think it would be correct from the information we have available.

DR. COMSTOCK: It just seems that the one group feels that by taking a population that has a narrow base -- well, they do a little selection, I guess, between these narrow-based populations and then they select ones to go into, and go into them and work with them.

DR. CRITTENDEN: Did you say the incross breeders were doing this?

DR. COMSTOCK: It was my impression.

DR. CRITTENDEN: It wasn't my impression from talking to some of them. There are a tremendous number they screen each year looking for a couple of lines that hit.

DR. COOK: But at the same time in these old commercial standard lines they are essentially following this program.

DR. COCKERHAM: I am completely confused now.

I have a slightly different impression in terms of 3-way versus 4-way crosses. At least I know a few people that are, they tell me, using 3-way crosses. I wonder what the relative proportion is?

DR. COOK: I do not have any information on what the relative proportions of 3- and 4-way crosses would be. But I do understand that the two major incross breeders are putting a 4-way cross on the market.

Now, we have in the so-called strain-crossers --some of these are 3-way. I don't have the information here as to the proportion of these.

DR. COCKERHAM: And the other thing that is relevant there -- they start out with some strains, but they work very hard when they find a good strain cross to improve it, which

involves either some sort of reciprocal selection or sub-lining and trying to get better combinations.

DR. COOK: I think that is right.

Right now when you look at it from a competitive standpoint, I don't know how you would pick the best one.

DR. COCKERHAM: I am not trying to pick the best. I am trying to understand what they do and also that they put out changes every few years, or every other year, almost. Is that not true? It will be almost the same.

DR. COOK: They come spasmodically.

DR. COCKERHAM: Somebody is lucky?

DR. COOK: Yes.

DR. KING: I have a comment I would like to pitch in for what it is worth. The random sample tests give one a good opportunity of making a little analysis of what the progress is that various breeders are making, and I have been making a study of this over the past few years. And it is interesting to look at the individual breeders, knowing what their system is, and to look at their progress over the years. And I think this gives some indication of the kind of breeding system they are using and how they are putting their results into their commercial product.

The incross breeders don't show any consistent trends over time in terms of progress. They will go along bobbing up and down relative to the control population in the test for a few years, and then suddenly they will make a change. And sometimes it is up and sometimes it is down, depending on whether they made a bad choice or not when they finally decided they had a better product.

Whereas, the strain-cross breeders tend to be more consistent in their progress. You can see changes being made from year to year, with very little fluctuation. And I think you can have a lot of confidence in this because the control strain is entered in ten or more random sample tests. This means upwards of a thousand birds or so being tested in different locations, and the same thing for the commercial breeders. And it is for specific traits that you see changes taking place.

For example, Heisdorf and Nelson started off their entry in random sample tests with about the smallest average egg weight of any commercial breeder in the industry and they actually were lower than the control strain. The reason the control strain was as low as H and N was that half of the control strain was made up

of H and N birds in the first place. It was a two-way cross at that time from H and N which made up the male side of the control strain.

But over the past 7 or 8 years there has been a constant trend of increasing egg weight in the H and N egg strain to the point where it is an ounce larger than the control strain now.

Honeggers was starting off in the test with some 12 days later maturity than the control strain and has made a consistent change in this age of maturity to the point where now it is about 8 days earlier than the control strain.

And similar things of this kind can be looked at from the random sample test results for the strain-cross breeders. You can almost tell what they are selecting for, what their emphasis is, by the change taking place in their particular stocks. But for the incross breeders you can't predict what will happen because they bob around and have no trends that you can see.

DR. BOVARD: I am confused about what inference we should draw when you said as soon as hybrid was defined it was dropped. Does this mean that because they had to be 37-1/2 per cent inbred to be called hybrids, that those using those had lines less inbred than that, or that they were much more and didn't want to admit it?

DR. COOK: I think I might answer your question this way.

First of all, it was very easy to switch to the incross designation without revealing any information, and in effect I suspect that this is what has happened. In other words, from the standpoint of the incross breeder, rather than continuing to advertise hybrids and then possibly having to back up this some time by revealing what he was actually doing, it was much simpler to go the other direction.

In other words, why reveal information that you don't have to? And I think this is the attitude they are taking.

DR. BOVARD: If you had to guess you would guess most of these lines are probably more than 37-1/2 inbred?

DR. COOK: I think you will find a lot of variability. I think you will find some that will have a considerable degree of inbreeding and probably some with a relatively low degree. I am just speculating.

DR. KINCAID: Now I am confused. What is the difference between the two, the line cross and the incross? They look to me like the same thing. They are both developing gene pools.

DR. COOK: They are both claiming to accomplish the same end.

DR. KINCAID: Aren't they using essentially the same scheme for doing it?

DR. COOK: Essentially with the exception that the incrossers apparently are doing some inbreeding.

DR. KINCAID: Well, they may or may not. They are just crossing lines of some kind, aren't they?

Panel Discussion:

Dr. N. D. Bayley Moderator
Dr. C. C. Cockerham
Dr. R. E. Comstock
Dr. W. H. Kyle
Dr. G. F. Sprague

DR. BAYLEY: Now, we have had a pretty good session of listening to the presentation of programs and plans in addition to the thought-provoking discussions of the four first speakers on our program. What happens from now on is up to everybody. One always plays this part of a program by ear. I am sure that Bob Blackwell didn't realize that he was giving me the text for this part of the program when he mentioned Hamlet. There are four points regarding his use of that quotation which I think have some pertinence here and now.

First of all -- and I am teasing him, of course -- I think the quotation was quite inappropriate. After all, research on inbreeding might be described as incestuous but I don't think any of the crimes were as heinous as those involving Hamlet. So I don't think the past is quite as gory or black or unworthy as the quotation might have suggested.

What about this past research? We have had some suggestions during our session that we might have been better off had we never done it. And I am sure that from others we also would have had suggestions that it was a worthwhile effort. We expect these differences of opinion, and I don't think it matters which conclusion we come to. I think we would all agree that whether this was a random walk of disordered investigation or whether this was a worthwhile and well directed effort to explore inbreeding in livestock, the way has been littered with productive papers involving information about our livestock, information on the effects of inbreeding and line crossing in all our classes of livestock.

I am not trying to suggest, however, that we should go on forever. And this comes to the second point in regard to the quotation from Hamlet: We do have a question. It has been raised here. Dr. Kyle plunged right into it when he said that inbreeding and line crossing was strictly for the birds, and he thought the birds (poultry) had abandoned it.

Dr. Comstock and Dr. Shelby also mentioned its limitations. And I will have to admit that I have never heard as much public denunciation of inbreeding and line crossing and the research related to it since ten years ago. At that time Milt Fohrman, in one of his routine but always heated debates with Jay Lush, finally puffed on his long cigar, blew out the smoke, and said, "inbreeding is like sin. Everyone has to get involved with it in order to find out how bad it is."

But that isn't the whole story, and it is obvious from the presentations that have been made here that there are differences of opinion regarding inbreeding and line crossing for livestock.

Dr. Brum mentioned some of the reasons that he has. He stated that we have a lot of information on mass selection and family selection but with dairy cattle we have very little information with regard to the possibilities of using inbreeding or the value of specific and general combining ability. He also mentioned the fact that with the development of artificial insemination we might have more use for this type of approach to livestock breeding than in the past.

Dr. Blackwell mentioned that one of the questions that came to his mind about the future of inbreeding research was the matter of realizing the investment which has already been made.

And beyond this point we have a factor which has been apparent to many in this group, but not brought out completely. This is the fact that in the 1970 projections for the Animal Husbandry Research Division, some of the branches have projected programs which involve nine professional man years on inbreeding and line crossing of livestock. Thus our Division has projected an expenditure during the next ten years of about $2 million to $3 million on this area of research. If the expectations regarding completion of this work, as given to me, are correct, we will probably add another 50 per cent to these amounts before the work is finished.

Furthermore, using the best estimates I can get from the livestock research study task force, the states have projections regarding inbreeding and line crossing which amount to about $4 million to $5 million worth of expenditures during the next ten years.

This suggests that we have plans for about $6 million to $8 million worth of expenditures on this subject during the next ten years.

Now, why do I mention this? Because I think this indicates that within our group somebody believes this is worthwhile, even though they may not have been heard up to this time. I think it points out that we have a real difference of opinion within our group regarding the future of this area of research, and therefore we should have a real vigorous basis for discussion.

Now, the third point regarding Hamlet: One of Hamlet's problems was that he didn't face the issue, and because he didn't face the issue I think you all know his end. And I can't get particularly inspired by avoiding this issue and facing Hamlet's end. So let's face this difference of opinion. Let's explore it among ourselves.

But let's do this in a semi-organized way.

First of all, I think we should proceed within a framework of the goals and purposes of livestock research. And in order to make those simple, I have boiled them down into two very broad ones:

First, the direct improvement of livestock; and second, contributions to basic knowledge of animal genetics.

Now, I consider the function of the panel -- as that of stimulants for the total discussion. They have their ideas and you have yours. The interaction of these will make the discussion a means of getting started, I will ask one or two members of the panel to present their ideas on specific questions. We will then let the other members of the panel react briefly and then we will have comments and questions from the rest of you.

The first question, that can be raised, is: Do the current and will the projected programs on inbreeding and line crossing contribute directly to the improvement of livestock?

I might just refresh your memory very quickly regarding what I mean by "current and projected programs."

In the dairy group we have the Ohio project on specific and general combining ability involving the development of four lines, which are being line crossed, with testing among them as the inbreeding develops.

The Minnesota project has the development of two female lines, and three sire lines, which also would be tested as they are developed for the possibility of specific and general combining ability.

Then, in beef cattle -- what is the total number of lines that has been developed? I couldn't quite get it from the discussion the other day.

DR. BRINKS: About 45, I guess.

DR. BAYLEY: And these will be tested for specific and general combining ability. Is that what you have in mind?

DR. BRINKS: That is part of our program.

DR. BAYLEY: I appreciate there are other aspects but I am talking about the inbreeding and line-crossing aspects right now.

Then with sheep there are the lines developed at Dubois which are now being tested. If I am correct, these are the current programs with which the Division is involved. I did not find any in swine at the present time, nor in poultry.

Now, this is just a brief explanation to state what we are talking about, and I suspect that not only our panel members but other persons will want to have more details on these as we go along, but we will see if this becomes necessary.

With that brief introduction, I am going to start by asking Ralph Comstock to lead off with a comment on what ways might these current and projected projects might be able to contribute to the improvement of our livestock.

DR. COMSTOCK: The problem in this sort of thing is often to stay on the subject, so I am going to make an explicit effort to talk in terms of the question you asked me as I understand it. I will first paraphrase the question.

When he says "direct improvement of livestock," I am thinking of the livestock used in the commercial production of meat and dairy products, perhaps in the United States, and a contribution genewise to the whole mass of livestock that is in our commercial production. This is what I understand by your question.

DR. BAYLEY: That is all right. We can start with that one.

DR. COMSTOCK: All right, I will answer that one. It seems to me the answer to that one is quite obvious.

We don't have the large centers of multiplication and distribution that Dr. Cook described for the poultry industry. It is, in the first place, perhaps it is not terribly likely that within a small number of lines one is going to be uniquely superior, and if there is one that is uniquely superior, there is some question as to whether it would be identified as such. Then if this were the case, there is a lot of reason to doubt that it would get effectively used to improve the Hereford breed or the Angus breed or the Targhee breed -- not that, I shouldn't say that.

So it seems to me the direct genetic improvement from this is likely going to be -- I hate to use the word but I will -- likely to be infinitesimal.

Now, he underlined --

DR. BAYLEY: That is the second part of the question; right? (Indicating blackboard)

DR. COMSTOCK: Well --

DR. BAYLEY: Through the development of new methods. Go ahead.

DR. COMSTOCK: Now I can pick up my notes.

DR. BAYLEY: I was afraid I had left him without a speech.

DR. COMSTOCK: I think that one of the most important things -- of course, you know I am way off base here because he says, "What is this going to contribute"? and I hardly know what he is talking about because I have had my nose in so much business or in no business so much that I don't know what all of you folks are doing by a good long ways.

It seems to me it is awfully important to be clear about what we are talking about, what are our purposes.

It says, "through development of new methods." This brings two ideas into my mind. One is to gain information that enables us by synthesis to come up with new methods; by deduction to come up with new methods; or, as a business of testing as comparing.

Now, if you ask about the scientific information that is going to be obtained, then I would just kind of like to almost leave it and say, "You people tell us what you are thinking about specifically, or more important, identify it for yourself so you know what you are doing."

We had a word or two said about the need to learn the explanation of heterosis, and this is not a new word. We have been puzzling about heterosis since quite a while before I was active on the scene, and in a way are no farther along than we were before.

Now, that seems to me very important. I do not think we are going to get the crucial answers about heterosis from the inbred line work with livestock. The crucial questions to my mind that relate to methods of improving livestock are, to be repetitive, the question of whether there is any important amount of overdominance, and whether there are some special highly active epistatic systmes.

And I don't think we will get the answers to those questions from this kind of work. I think we have got a much better chance of getting it, if we have any chance anywhere of getting it, from work with laboratory animals, and I think it would be highly desirable if all of us got behind a program of doing work with laboratory animals that seemed to have a chance of giving us some new information in that connection.

Now, on the other part of this -- I want to say a word here because it seems to me there is some confusion in my mind and it seems to me there may be some differences in thinking in the minds of other people here -- Dr. Cockerham has been trying to get at this.

When corn people are talking about the inbred system, they are talking about developing inbred lines and selecting among them, selecting among them in this case primarily on the basis of their performance in crosses. They have really no thought of selecting within the lines and improving, making the lines better by that selection, or very little thought of doing that.

If you are going to take that point of view that you are going to make your accomplishment between lines, then you have lines to select among, and even with beef cattle with 45 or 50 it is a far cry from the number of lines that have been developed in corn and perhaps a number of the lines that these large poultry breeders have taken a look at.

And Dr. Cockerham's initial talk indicated you don't help your selection very much selecting between lines unless you get that inbreeding coefficient up so the variation among lines amounts to something.

So on the basis of numbers of lines and talking in terms of something that would give you an improvement that you could see and cite as something tangible to breeders and say, "Here we did something; this is a way to do it," I don't think you give the system a chance, and a number of people would say "We can't give the system a chance because it takes too long to develop the number of lines that justifies the between-lines approach."

Then the other approach is to use the inbred line as a device for making the ordinary kind of selection more important, in other words, close the population so you can get everything on the population and get straight-out kind of selection of the kind people have done for so many years.

I couldn't be quite so pessimistic about the chance of this being effective except on one ground, and that is one of, say, experimental design. Do we give this a real chance of showing something? Do we have the controls that we need? In other words, have we minimized that probability of error of the second kind that Dr. Blackwell was talking about? Have we got it down low enough so that if somebody does do a pretty good job of selection within an inbred line and comes up with one that is pretty good, it is going to get tested enough, and under the circumstances that will enable it to show it is good?

I would like to say one further word -- and maybe I will have a lot of stuff off my chest.

I might be accused also of trying to say everything I had heard, stealing other people's thunder.

What I was going to say was I think one of the definite accomplishments in the last two decades in animal breeding is in education of animal geneticists. I think there has really been something accomplished by getting people who know quite a lot more about quantitative and population genetic theory of the kind that was set going by Dr. Wright and Dr. Lush and so on, and we have enough people with that sort of knowledge so that this is a real accomplishment, and I think one of the most important things that should be in our thinking now is to capitalize on this, and how can we do it? We can do this in a lot broader general statistics training. We can do a lot better job of identifying objectives, working out a reasonable approximation to the differences it is fair to expect between two different procedures -- do a little design and thought statistically as to what is our chance of showing what is the kind of difference that we have a right to expect, and where are these differences likely to be in the light of what we now know and in the light of the knowledge of theory we didn't have a while back when a lot of this was set in progress.

DR. BAYLEY: Dr. Sprague, would you like to react to this question from the standpoint of your experience and background?

DR. SPRAGUE: Since Ralph was very formal and stood up, I think I will stand up, too.

DR. BAYLEY: You don't have to.

DR. SPRAGUE: I would like to make two comments before I start in. The first one is that Ralph gave half of my speech --

DR. COMSTOCK: I just wanted to see how good you were at thinking on your feet.

DR. SPRAGUE: And the second one is that I don't know anything about livestock breeding in the first place, so I am going to extrapolate from corn and you can accept or reject the extrapolation completely as you wish.

I have a feeling that a considerable part of the interest in inbreeding and line crossing in livestock is, to a considerable extent, a direct outgrowth of the experience and success that has been obtained in the hybrid corn program. I think, though, that that is about as far as it goes. There have been several points that have disturbed me very much through the course of the meeting, along this general line.

First is the emphasis on inbreeding depression. This I don't think -- well, within limits, of course, it is important but I don't think this is the important aspect of it.

If you develop from any random mating population, if you develop a large number of inbred lines, even with a considerable amount of selection involved, and then recombine these inbred lines, you are going to get back essentially to the same base population from which you started. And of course if the number of lines is very small there is a possibility for considerable departure from this base.

The other point I think has been completely overlooked -- maybe not completely overlooked in thinking about it, but at least in practice -- is the tremendous scope of the corn program, which has permitted the progress that has been made.

In the development of inbred lines in corn we do some selection during inbreeding. We don't feel that this selection is of tremendous importance as far as the performance of the hybrid is concerned, necessarily, but it is of very great importance as far as whether a particular inbred line does or does not have any possibility of having any commercial use. In other words, we have learned from bitter experience that the combining ability of an inbred line that is difficult to maintain is of academic interest only, because there is no possibility of using such a line. So that in the course of inbreeding, the selection is primarily on: Does this line have sufficient vigor -- and I will use "vigor" here in a very broad sense -- so that it can be maintained easily enough so that if its combining ability is good there is some possibility of using it commercially?

Then the other thing I think may be overlooked by people who haven't had too much experience in corn is the tremendous scope on which the inbreeding and testing has been done. I am going to pull a couple of figures out of the air. I will make no great claims for their accuracy. But I think they are at least of the right order of magnitude.

First, if you could guarantee a corn breeder that he would get one line which was usable in commercial hybrid production out of each hundred inbred lines that he started, he would be very, very happy. And I don't have to have one inbred line; you have to have four if you are to produce a double-cross hybrid.

Then we made a survey not too long ago of the fate of inbred lines that have been released by the various federal and state cooperative breeding programs since 1948.

None of these lines were released except as they had demonstrated above-average performance in hybrid combinations. And what we were interested in was: What was the fate of these inbred lines? How extensively were these currently being used by the hybrid seed corn industry? Because I am sure you all know that practically all of the hybrid seed being produced and sold is being produced and sold by private industry.

And the figure here would be something in the order of one in ten of these lines that have been released on the basis of very extensive experiment station testing. And only one of ten in these has had sufficient merit so it has stayed in commercial use for any period of time.

So if you take the one in 100 figure and the one in ten figure, this gives you a value of somewhere around one in a thousand. This is one in a thousand for one inbred line. If you are going to produce a single cross, you have to have two lines and if you want to produce a double-cross, you have to have four.

So this gives you a little concept of the tremendous amount of effort that has gone into the development of inbred lines, which in turn is responsible for the success that hybrid corn has had in recent years.

Now then -- I am not saying that exactly these same figures would hold in livestock, but I think if you aren't prepared to develop and test numbers of lines somewhere in that general area, there is very little possibility that you are going to have much of any impact on the first point that is on the board there, the direct improvement of livestock.

DR. BAYLEY: Dr. Cockerham or Dr. Kyle, do you want to react to this at this point?

DR. COCKERHAM: No, indeed.

DR. KYLE: Only to say I agree with him very much, that it is a hopeless outlook as far as livestock is concerned, at least with our group. If we expected to get even one outstanding inbred line that would be useful commercially and not numbers under way at present, or have been started, it would be insufficient to expect more than one, certainly, just the chance occurrence of that.

DR. COCKERHAM: I think I should point out that I do agree, for fear that someone may go away from here saying that I am a hybrid individual in view of some of my earlier comments.

These comments were not meant to be that the hybrid procedure was a good one, but that decisions involving inbreeding and making hybrids don't really rest on inbreeding depression and heterosis, but rather on the ability to make a lot of hybrids and choose the best one.

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DR. BAYLEY: Dr. Cockerham's reference to being a hybrid individual impels me to comment that when I was a graduate student at the University of Wisconsin, I thought that I would become a hybrid individual by merging the contributions to my professional growth both from the genetics department and the department of dairy husbandry. Unfortunately, the relationships between those two departments in those days was such that I soon found out that my status was more like that of the German word for hybrid, "bastard."

We have had the reaction from the panel in regard to this particular question. What do you think? How would you answer this question among yourselves?

Keith Gregory, you have been pretty quiet.

DR. GREGORY: I think that most of the talks involving all the species have indicated a reasonable amount of non-antigenetic variation, heterosis, involving many of the traits with which we are concerned.

I would like for Dr. Cockerham specifically to comment on procedures which we should be exploring in regard to utilizing non-additive genetic variation more effectively in our breeding programs, specifically what knowledge do we need to acquire, what areas should we be concerned with?

DR. BAYLEY: Do you want to try that one?

DR COCKERHAM: He turned that one around quickly, didn't he?

I think really to answer this is required some knowledge of the gene action in terms of whether over-dominance or some sort of balance -- I will put it in that terminology -- I believe Ralph used multiple epistatic peaks -- whether these things are involved as opposed to just dominance, partial to complete.

Remember, you will still get inbreeding depression and if you get inbreeding depression you will get heterosis.

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This could be viewed from partial to complete dominance, or it could involve heterozygosity, shall we say, per se.

Any of your family mass selections will work, and probably are most efficient for anything less than balance. If over-dominance or other types of balance are important, sufficiently important -- you may ask me what I mean by that, and I am not sure -- then you must, to utilize this, to arrive at the best genotype -- you are forced to some system which can build for you or select among all kinds of genotypes involving heterozygotes.

The systems are reciprocal selection and developing lines and making hybrids.

What you are doing in essence when you develop lines -- if you will take your lines to homozygosity, if you want to think of it this way, you then have the possibility of developing genotypes, which you can duplicate. This means you can test, essentially make clonal selection by sufficient testing -- and incidentally this subject hasn't really been emphasized enough. If you can't make lines you can't test them, because this is what the corn people ran into. They could make lines, but they sure had a job testing.

But back to my story: If you do, then you are essentially making clonal selections and you are selecting among genotypes regardless of their genetic constitution.

This may be important if -- it goes back to gene action -- if you have balance or heterozygous combinations that give you the best genotype, then this is the system which will utilize this kind of gene action. The reciprocal methods will.

Now, let's say we have some of this and some of that, which is most likely the case. And then we must start talking about efficiency of various systems.

Now, if you cannot make a lot of lines and try them in a lot of combinations, then that system is out of order. That doesn't mean that you can't make some progress from family selection or mass selection for those genes which are not completely heterotic. And I think Ralph mentioned earlier probably the magnitude of a reciprocal system is such -- that is, the magnitude of the experiment that is required -- is such that you probably cannot cope with this; you don't have the facilities to have any chance of this being an efficient system, which would also make use of heterotic-type gene action.

So I think it is a matter of what you can do in terms of the facilities and so forth that you have.

That is a long answer. Is it the type of answer you were interested in?

DR. BAYLEY: Is that answer completely compatible with the unanimous views just expressed by the panel?

DR. COCKERHAM: In terms of present facilities, I would say yes.

DR. BAYLEY: Are there other comments?

DR. KYLE: In relation to what he said in asking the question, I wouldn't agree that most traits in beef cattle, at least, show a lot of heterosis. Certainly the ones on reproduction do, but I got the impression there was at least a lot of slaughter traits -- or was that swine -- that were highly heritable. And I believe the growth rate -- there was some heterosis in beef cattle but I don't have a high heterosis except in rates of reproduction. It seems to me you can get the heterozygosity you need if you are developing selective stocks that are distinct and different. In cattle you have the breed separation, but even within breeds, if you develop distinct populations, strains if you like, that are selected in different ways perhaps but at least kept separate and not intercrossed until you are ready to test a number of these -- and here is where you need the large facilities that Dr. Hodgson was asking about yesterday, to test these at a given location and see which are the best strain crosses, so called, without going through the matter of inbreeding except in so far as it occurs with limited population size in your selected strains, but developing many of these as possible -- I know this is a limited number -- but you can test strains which are of a size, then, that are useful commercially if this is what you want to do, or just test method. I think this is a critical point on whether you are testing methods and approaches experimentally to let someone take over on them, like commercial breeders, or whether you are trying to improve the animals themselves and make them available commercially. I think there is an important difference here as to approach.

You can go a lot farther on experimental approaches if you are not so concerned with those animals themselves -- and there are many things that could be tried that have not been worked on much yet, I feel.

DR. GREGORY: In answer to the premise in regard to the importance of heterosis, certainly there is a sizable heterotic effect, primarily because of the reproductive performance. But I would interpret beyond that the statement to the effect it is a matter of lines, inbred lines -- that is one of degree in your terminology. Is that correct?

DR. KYLE: Yes, I would say so, that with limited numbers you are going to have at least a tiny amount of inbreeding, or do already, in your breeds. It is variable.

DR. GREGORY: There can be barriers, yes.

DR. KYLE: But separation as far as possible to keep this low, and distinct populations selected that can be crossed to be your commercial stock.

DR. WILSON: I would like to direct a question to the beef cattle people. It seems we have struggled around, crossbreeding successfully all the way, and there has been little talk about it. It seems to me in a situation where we are hurting for facilities and money and so on, the crossbreeders would do very well. What would be wrong with simply producing strains highly selected for your heritable traits, such as carcass traits, ability to gain, efficiency of gain, and simply crossing these strains -- the strains, in other words, being in different breeds.

DR GREGORY: Of course there is considerable thought in this direction and programs being oriented in this direction. Actually, from the standpoint of heterotic effect on growth, it is in the neighborhood of approximately 5 per cent. Carcass traits are zero when adjusted for weight effects.

Fertility, of course, is up in the neighborhood of 12 to 15 per cent -- speaking now of breed crosses.

DR. WILSON: I think maybe you missed part of my question because the question was directed in such a way that you should make your strains, I will say, superior for these traits where you said there was little heterotic effect. You are not looking for heterotic effect in carcass traits. You produce this before you put your strains together.

DR. GREGORY: You are getting an argument among beef cattle people on that point.

DR. WILSON: I was thinking of an efficient way, with our limited abilities, in which you might produce excellent commercial animals.

DR. GREGORY: We have been investigating methods of selection and methodology involved in measurements to make it more effective specifically for these traits you mentioned. But over and above that we do have an interest in heterotic effects on these traits that we do not get a selection response to.

DR. COCKERHAM: These were breed crosses you were talking about?

DR. GREGORY: That is correct.

DR. COCKERHAM: Have you done three-ways?

DR. GREGORY: From the standpoint of evaluating heterosis effects on cross-bred with straight-bred dams -- so we are in the process of doing that. Data are accumulating. I mentioned fertility coming out of this particular segment or phase.

DR. COCKERHAM: If you pick your best combination there you can probably sub-line and improve on it for another 7 per cent but that again involves paying money.

DR. GREGORY: Yes. Another point I think is extremely pertinent here is the difference in magnitude of the heterosis effects involving different breed crosses, with just three breeds involved, Hereford, Angus, Shorthorn.

In other words, the heterosis effect on some traits, particularly the growth traits, are being almost twice as great in part of these crosses of the three than in the third cross. This has, we think, a real bearing on what we are concerned with.

DR. COCKERHAM: I would like to make the assertion, and possibly be corrected on it, that the entire success of the poultry industry as it operates, to a great extent, depended on there being available many closed flocks. As I understand it they still haven't tried them all. And this was their base. And they have been able to improve somewhat upon this in finding -- that is, it was their base in finding those best combinations. It was already done for them.

DR. SIERK: Both Stan and Wendell and, I think, others have used the word "strain" and "development of strains," the implication being at least that here there is a difference between a strain and a line. In other words, you prefer not to use the term "line" in this connection and I am assuming when you say "line" it means inbred.

DR. WILSON: I think generally, myself, the strain is breed lines --

DR. SIERK: Okay. A larger population than you would otherwise have.

DR. WILSON: Yes.

[illegible]RM: From the standpoint of evaluating heterosis [illegible] with straight-bred dams -- so we are in the process of [illegible] the [illegible] are accumulating. I mentioned [illegible] coming out of this particular segment or phase.

DR. COCKERHAM: If you pick your best combination there you [illegible]bly sub-line and improve on it for another 7 per cent [illegible] involv[illegible]

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DR. SIERK: Both Stu [illegible] Wendell and, I think, others [illegible] used the word "strain" and "development of strains," the [illegible]lication being at least that here there is a difference between strain and a line. In other words, you prefer not to use the term "line" in this connection and I am assuming when you [illegible] "line" it means [illegible]ed.

DR WILCOX: I think generally, myself, the strain is [illegible] lines --

Then I would submit that basically it seems to me in the large animals, beef cattle, swine and sheep, this is primarily what people have been engaged in. Is this not correct? They have been engaged in this in developing strains. Maybe they haven't been going at it in the right way and perhaps some of these people have some suggestions here as to how this might be done, but I would say that primarily, at least in the beef cattle, this is a matter of developing strains rather than lines.

Now, what is the difference?

DR. SIERK: And it is the reason why I think this blanket that has been thrown over inbreeding -- maybe, as I say, it is one of degree -- should be defined a little more precisely.

And I would come back to the figures put on the board at the beginning, that I would question a little bit whether the amount of money -- after all, it is just money so I don't feel it is important -- whether that amount is justified in saying this is used for inbreeding and testing of inbred lines. I don't think this is correct, if I may be so bold as to say it, that it involves more than this, considerably more than this.

DR. BAYLEY: There were breakdowns in the Task Force outline which considered other aspects of line development than this. Therefore the figures put on the blackboard should reflect inbreeding research.

DR. KING: Unless I have missed the point in the description of these inbred lines of dairy, beef and sheep, it seems to me they are talking about a different thing in these large animals than we are talking about in poultry when we speak of the strain, as Dr. Wilson mentioned. Because most of these lines that you are talking about for large animals are one- or two-sire herd propositions, where the only reason that inbreeding is still relatively low is because you have such a long generation interval.

In 35 years' work in poultry you would have accomplished 25 to 30 generations. And when we are talking about a strain in poultry we are talking about early practice when we had a large number of these developed, somewhere between eight- and 20-male flocks. Now most commercial breeders are talking in terms of 16 to 50 males for each of their closed lines that are under development, and their main ones may be 100 or 200 males heading up each flock. So I think, although inbreeding is going on in the development of these flocks, it is going on in poultry at a much faster rate than in these one- or two-sire herds.

DR. COCKERHAM: I would like to have something clarified, though. These lines have to be built up to be used commercially and sometimes in their history they were much smaller -- or that is, inbreeding is much larger than that would indicate.

DR. KING: In poultry?

DR. COCKERHAM: Yes.

DR. KING: The inbred lines you are speaking of?

DR. COCKERHAM: Yes. You can have a 2500-sire line that is homozygous.

DR. KING: Not the inbred populations but the so-called strains of inbred populations. Most of these did go through a bottleneck in it earlier, somewhere between 8 and 20 males, and sometimes even less than that. But it is not this long-time proposition of only one or two sires each year.

DR. BAYLEY: May I clarify something that Keith Gregory mentioned? In regard to the blanket over inbreeding, I am sure there is no intent here that incidental inbreeding related to other objectives is under discussion at this moment. The panel has been primarily involved with the development of inbred lines for the purposes of obtaining a hybrid. Isn't that correct? And the panels discussions and reaction to these programs is about those aspects which might have this intent.

Is that correct?

DR. COMSTOCK: Yes.

I would like to ask a question now of the group. I expressed somewhat as an opinion -- I think I did and Dr. Sprague certainly did -- that with this number of lines the business of selection between lines unaugmented by improvement of lines by within-line selection had no chance of accomplishing anything. And when I say "no chance," remember, it is a matter of degree, but it is relatively low.

Does someone want to argue with this? I think we might seal a point or see if it is sealed.

DR. BAYLEY: Do you understand the question?

DR. KING: State it again.

DR. COMSTOCK: I tried to describe when I talked before that there are two ways of looking at this, the use of the inbreds or strains, or closed populations. The one thing is, as the corn people have emphasized, the selection between lines, and that this has accomplished a lot because they had a lot of lines -- Dr. Sprague emphasized it -- they had a large number of lines to select among so they could find one at the end of the distribution, or a hybrid out at the end of the distribution. With a small number of lines the possibility of getting a top one will be pretty small.

The other side of this is that there be a lot of selection within lines. And this is another kind of an issue. This is another kind of an approach. The inbreeding plays an entirely different role here. And the question I am asking -- I said that if the first approach, the emphasis on selection among lines is going to accomplish anything, is going to be productive, there have to be a lot of lines and we don't have them in livestock and probably we won't have them, so that this aspect of it is not going to amount to much.

Is there agreement or no disagreement.

DR. BRINKS: In the case of beef cattle the only place I know of where between-line selection would be is at Colorado where they have had maybe 16 lines and from this 4 or 5 lines have emerged with general high combining ability. I think this past inbreeding has been a matter of picking out genotypes that have high combined qualities for growth which is important in beef cattle. There has been no selection, I think, for specific combinability that I know of.

In all the other lines I would say inbreeding has been within strain or in-line selection. In these highly heritable things it seems in-line selection has been effective in overcoming the effects of inbreeding. It looks like we have made progress for highly heritable traits. Then I think we get to the point Stan made, that we have selected several strains with traits such as growth, and maybe carcass traits -- but in combining these, going down the line and testing for the top crossing program, we get at the amount of heterosis and other things you mentioned.

DR. COMSTOCK: Did you agree or disagree with me?

DR. BRINKS: I agreed with you except that on the point about the limited facilities, we can't have a lot of inline selection except for selecting out a few lines with specific combinability.

DR. COMSTOCK: What does that do for you? Let's say you improve the lines a little bit over what they would have been had you not selected. What does that do for you?

DR. BRINKS: I think for the highly heritable traits such as growth, then by crossing these we can obtain something higher by increasing reproductive efficiency and so forth from the heterozygosity.

DR. COCKERHAM: I won't agree with that and I don't care whether you select in lines, among lines, or on the basis of their general combining ability, you will get some improvement in your crosses as reflected from the mean of the population you are starting with. But you are working on the same kind of gene action as you would be when you are doing mass or family selection. Then it becomes a matter of efficiency and I think Ralph's point -- if this is what you are going to work on -- do you see what I am trying to say?

If this is what you are going to work on and if you are selecting within lines or among lines or on the basis of the top cross performance and so forth, then you are working for improvement that you could get by selecting within the population by mass or family selection and it is probably much less efficient. You can't hope to take advantage of dominant gene, and things like that, over-dominance and so forth, by this procedure.

DR. BRINKS: Why not dominance?

DR. COCKERHAM: Heterozygous action. Now the corn people have gone beyond this. They are concerned somewhat about the effect of selecting lines -- they know they are going to improve the mean of the hybrid, but they are concerned about the distribution of the hybrids. Therefore they look at high lines by higher lines and high lines by low lines, and things like this. There is no question they are going to improve the mean of all their hybrids, but they may mix the distribution so their chances of getting a top hybrid, you see, for over-dominance -- you would mess up the distribution so the chances of getting a top hybrid by selecting on the lines could be less.

DR. BRINKS: I will agree with this but are we this far down the road on beef cattle? Aren't we right now involved in improving the hybrid?

DR. COCKERHAM: I would like to point out, to talk about lines with inbreeding of 20 per cent you are absolutely guaranteeing that these crosses are going to fall right on the population mean with very little distribution around it. You can't hope to find your hybrids to have any variation among them to specify. You are almost guaranteeing that the thing is centered right on the mean everytime, except for this within-line and so forth selection that has centered you just a little bit above the population mean, but you are still centered there.

DR. BRINKS: But if you do make progress between lines and get 5 per cent heterosis, aren't you moving in an upward direction at a fairly rapid rate?

DR. COCKERHAM: Wait a minute. You have to compare that to something.

DR. BRINKS: Yes, this is it. I am not saying this is the optimum --

DR. COCKERHAM: I really don't know what your facilities are. You are not going to do a lot with a 25-cow herd and a couple of bulls with any kind of selection system. You talk about this one consequence of within closed population selection, and that is inbreeding, and it doesn't do you a bit of good from the standpoint of animal improvement to select and correct for inbreeding and say, "I would have improved had I not had inbreeding" because you are stuck with what you wind up with.

DR. BRINKS: Yes, but most of these things have shown some response to selection.

DR. COCKERHAM: I think so, yes.

DR. YOUNG: I am not sure what the argument is about but as far as dairy cattle are concerned I would like to express my opinion anyway.

In the case of dairy cattle breeding, I think we can say fairly safely that a sire could be identified with a line. In other words, since a bull through artificial insemination can leave 50,000 or 100,000 offspring, I think we can claim a sire is actually a line.

And in the case of dairy cattle breeding, because of artificial breeding we can rather accurately estimate general combining ability, so for these particular sires we can estimate that. And since these bulls that have high general combining ability are the ones that are going to determine the genetic pool in the future, there is certainly not much point in our fooling around with any bull that doesn't have high general combining ability. But among these bulls I think we would be quite interested in knowing whether there are combinations of these that would show something in addition to just this high general combining ability.

For the present it doesn't make a whole lot of difference, because there is plenty of additive genetic variation and we are moving forward rapidly -- I don't think many people realize how rapidly.

But it is possible that this genetic variation may tend to be reduced and at that time I think it is rather important or at least would be worth knowing whether there is any specific combining ability. So, as far as I am concerned, this is the major reason that we are interested in things of this nature. I don't know if this has anything actually to do with the discussion.

DR. BAYLEY: Dr. Young, in his comment switched us away from the beef cattle discussions over to the dairy. He mentioned that he considered that a sire and his progeny could be identified as a line because of the tremendous number of progeny which occur from individual bulls through the use of artificial insemination.

Dr. Brum earlier referred to the impact of AI on dairy cattle breeding and suggested this is one of the reasons why we might be interested in looking at some means other than mass selection for the improvement of dairy cattle.

I would like to get another reaction to this and maybe Bob Lamb would be willing to comment.

DR. LAMB: Probably my reaction would be more from a personal observation than any data we have to go on.

First of all, I would agree with Dr. Young on his thesis here, though in dairy cattle we could consider this a line. I think one of the things we are observing in dairy cattle is through artificial insemination we are tending more and more to develop these lines. One bull becomes very popular in AI because he does have apparently some general combining ability and apparently a large number of bulls that come into AI are related to this bull. All of his sons are immediately stamped and given heavy service. I think in our Holstein breed it will be a considerable time before we run into problems on this but I can see problems starting to arise in our breeds of smaller numbers.

I think this needs to be of concern to us, whether we will be able to keep a broad enough genetic base to make progress in these breeds.

DR. COCKERHAM: I would have to state my objection to his progeny being called a line from the standpoint that a line, whether you stretch it to include strains and varieties, at least these have one thing in common, they are closed on both sides of the pedigree, that is, the male and female side. So if you want to close this progeny from then on as a line, I wouldn't object, but otherwise I don't think it should be termed a line.

DR. BAYLEY: In other words, it needs to go beyond just the sire-daughter generation. Is that what you are getting at?

DR. COCKERHAM: Yes.

DR. BAYLEY: Any reactions to this point of view?

DR. KYLE: I would agree with that. I would also agree with the previous speaker, that the dairy people had better start making long-range plans to keep separate strains, so-called, on the basis I was talking about earlier, or they are going to have problems in holding fertility at a high level, because eventually this will narrow down more and more with widespread use of artificial insemination, and as you pointed out, many bulls for the next generation coming from a single bull in this generation. And I think you need to have some long-range plan for keeping parts of the population separate so that in the future these things can be crossed, or you are going to get to a single homogeneous population, so-called, in which you have -- well, just like one lowly inbred line. And this heterozygosity, particularly for reproduction, is needed.

Along the line of strains, I think there was quite a bit of difference in terminology earlier about this in beef cattle and I think the whole point of view would be different if you were thinking not in terms of inbred lines but in terms of selection in non-inbred populations. I believe in places like Colorado you would be going to larger groups in which there was no intent to inbreed just whatever occurred, but the populations for selection would be larger. You would be using more sires in a population. They would be a closed group and then crossing these groups, strains, if you want to call them this, whatever your terminology -- but the purpose is quite a bit different. I think in your beef cattle your average size of line, so-called, for efficient selection procedures these would need to be considerably larger. This is the difference.

The point of view would be different on these purposes.

DR. YOUNG: I just was thinking if the population is going to run into trouble it is a good thing we have these inbred lines so we can bail it out when it gets in trouble.

DR. KYLE: They may not survive.

DR. WARWICK: I would like to raise a question that may be a little bit afield from what we have been talking about, and I would like to have comments from the panel, perhaps particularly Dr. Sprague and Dr. Comstock on this type of question: Heterosis in our meat animals or large animals is real, and it appears in all likelihood we are going to be taking more advantage of it in the future.

Are we going to be limited to the use of heterosis that occurs fortuitously in the populations that we have access to, and if not, what suggestions would you have for improving the degree of heterosis, if we can use that term?

And then, a related question: Should we be engaged more actively than we are now in being germ-plasm explorers all over the world, hunting for breeds, types of livestock that will give a greater heterotic response with other breeds than we may now have?

DR. BAYLEY: Who wants to try it first?

DR. COMSTOCK: Well, you know I got carried away by wondering who was going to answer and I hardly heard all the question. I will go up here just for a change, to the blackboard.

On this thing of should we be germ-plasm explorers, I think the only thing I can say is "Gosh, I don't know."

I gave a talk to -- what do they call that trade?

DR. SPRAGUE: American Seed Trade Association.

DR. COMSTOCK: Yes. And I thought a lot about this question and it makes a good story, you know, that out here in some foreign breed there must be some genes that will do us some good. I am just as sure as I am of anything in the world that that is true. But how you separate them out from the ones that you don't want that will do you some harm, I don't quite know, without a tremendous effort.

Now, it seems to me they can't be in the category of, "They ain't much good by themselves but they've probably got some good genes in them." That is a hard role to exploit, it seems to me.

Now, I am going to try to connect what I think was your earlier question, and I think that was about what you do about improving combining ability -- try to connect that with Keith's question in my own frame of thought, and I want to do something else, too. I want to connect this inbred hybrid system to reciprocal selection and show a tie-in here.

If you just go and develop inbred lines and cross them and find the best hybrid, identify it or several of them, once you have done this, and done it with a large number of lines, it becomes less attractive to go back and do it over again with the same number of lines from the same source, because you already got a ways out toward the end of the distribution and it will get harder and harder to get farther with the same number of things you have been trying. It is the old story Dr. Sprague has emphasized many times.

Then you have to think: What are we going to do? One of the things you say you might do is to take these superior hybrids, the lines that are involved in the superior hybrids and put them together in another population and start from there. But one of the things that happens when you do that is your original selection for specific combining ability isn't all fruitful in terms of your improvement of the base population, because it was the additive genetic portion of the game that is more useful for that.

So I say it is better to have developed lines that you can put in two categories, as one category being a little more related to each other than the other. Say you developed lines of Angus and Herefords and made crosses among them and the good Angus lines you mix together and the good Hereford lines you mix together and got a new Angus breed and a new Hereford breed that combined a little better as a result of this. Then you would be doing reciprocal selection.

I want to point out that the connecting formula, which I am sure Dr. Cockerham knows, is a formula that he put down when he gave you yesterday morning a 1-plus F multiplier, where F is the inbreeding of the lines, so when we talk about inbred-hybrid procedures as against reciprocal selection, we can talk about them as being the same thing if we want to look far enough into the future. Then the question becomes -- if we get completely inbred lines, our expected gain per cycle of selection is twice what it was before, without epistasis, and we have used a lot of time getting up to this "F equals 1" so that we have doubled this.

So there is some question as to whether that is worthwhile. So this drives me back towards the idea that if you have to do something about specific combining, I am still going to say I wish you would think real hard about: Is there any way -- now, remember, I said if you really have to do it. I am not convinced that there is so much of this non-additive variance of a particular type that

it is going to be worthwhile, at least for a long time. I just don't know the answer to that. I don't hardly think so. But if you are convinced you have to do it, then I want you to think real hard about reciprocal selection and you have to think about somehow organizing a facility -- whether it takes cooperation between several breeders -- how do you sell them on it? But you have to have a program that is big enough to work from, if there is such a thing in beef cattle.

And I did have the one reaction, Keith, to the thing you said, there is a lot of evidence for non-additive genetic variation, and I am not quite sure there is much evidence to indicate this is of the type that arises from over-dominance or epistasis, though I don't doubt there is some of that.

DR. BAYLEY: Dr. Sprague, do you want to comment further?

DR. SPRAGUE: I would like to make just one comment, I think. It may be that I am confused on this, but I get the feeling that there have been several implications at least that if you can demonstrate heterosis then you must have, in fact, demonstrated dominance or epistasis. This is not true at all. You can get heterosis with genes that are partially dominant, if you have enough genes which are behaving in this particular fashion. And this may very well account for most of the heterosis that we have observed. And this type of gene action would be amenable to a mass selection or various types of family selection.

So you would need a good deal more than just a demonstration of heterosis to say that you are vitally concerned or you had a considerable amount of non-additive genetic effects involved.

DR. COMSTOCK: I just want to say "Amen" to that. Remember, Crow pointed it out, you can get all kinds of things with just dominance or partial dominance.

DR. TYLER: Yesterday, Clark, you indicated, I believe, that if the regression of inbreeding depression on degree of inbreeding is linear that indicates partial to complete dominance -- in other words, if it is straight linear.

DR. COCKERHAM: No. I might have left that impression but if I did, it is wrong. If it is linear it says that it is in terms of dominance effects, but it doesn't tell you what kind, partial, to complete to over-dominance.

You see the problem is that we as yet have no techniques to provide substantial evidence on the question of over-dominance or multiple peaks versus partial to complete dominance. We have not been able to make this distinction even with the techniques involved, and some special ones in laboratories.

DR. COMSTOCK: Clark, I want to take exception to that. I feel the North Carolina work with corn does bear on this subject of over-dominance.

DR. COCKERHAM: Well --

DR. KYLE: If there is epistasis?

DR. COMSTOCK: Well --

DR. COMSTOCK: Let me remind you in open pollinated varieties of corn that presumably have been under some selection for a while, they found about twice as much additive genetic variance as dominance.

DR. KYLE: How much epistasis?

DR. COCKERHAM: Now, Ralph, I think I will agree with you in principle, but when I said real distinctive techniques, that takes care of all kinds of possibilities. I am still going to stick to my guns.

DR. COMSTOCK: Then I will ask one question --

DR. COCKERHAM: Just a minute. Let me finish.

And I will draw now on the results from corn. There have been lots of studies, making inbred lines, random lines as much as possible, using various techniques of estimation and so forth, and the results so far -- there is always a loophole because the inbred lines are certainly not quite the random sample that they are assumed to be -- but all the techniques so far that we have do indicate no epistatic variance to speak of. I will have to admit that. And with that evidence -- and that has been obtained fairly recently. If you go back then and look at some of the earlier results in terms of degree of dominance and things of this kind that have been estimated using corn, the average degree is less than overdone. But still, Ralph, that doesn't exclude -- and there is no way to really say about relative amounts, I think.

DR. COMSTOCK: Well, I suspect I am more naive than I ought to be, Clark, but when it was discovered in the openpollenated varieties of corn that the dominance variance was considerably less than the additive variance, I did conclude that there was a lot of non-over-dominance. And I still am stuck with this feeling.

DR. COCKERHAM: Yes.

DR. COMSTOCK: I do admit, of course, that I haven't excluded the possibility of some over-dominance.

DR. HETZER: I thought I would like to be corrected on one point if I should be wrong, but it does seem to me Crow pointed out any heterosis above five per cent would have to be explained in terms of over-dominance.

DR. COCKERHAM: I want to take that on. The assumption there hinges on deleterious genes being held in the population by mutation only, you see, at the frequency that there would be an equilibrium between selection and mutation.

Now, you see you have different strains. These are inbred. What he is talking about is a terrific conceptual population that has evolved over time under some constant scheme. Now, the reason you get heterosis between these strains, breeds, and what-have-you, as far as I am concerned, means that these are not equilibrium populations generally.

DR. HETZER: That means selection has not operated against those.

DR. COCKERHAM: Some genes are fixed, you see, between them. And it just doesn't make sense to me that in practice you generally have equilibrium populations at all. They have been selected over time for different things.

So I don't think this really bears on this.

Now, given the assumption of the conditions he had, you are quite right, but I don't think you ever have them.

DR. COMSTOCK: But the assumption is wrong by the very fact there is additive genetic variance and that selection of the kind that Gardner and Lonquist have done has improved corn varieties.

DR. COCKERHAM: But I was talking about just his deleterious genes, 5 per cent. But it goes on over.

DR. COMSTOCK: But if that is the point, they are all in equilibrium, Clark, and if they were, Gardner and Lonquist wouldn't have made progress.

DR. COCKERHAM: Right, right. You just don't ave populations like that.

DR. BAYLEY: I am going to push this discussion in a slightly different direction. There have been several references in our comments, both from the group and from the panel, regarding efficiency of systems or methods of improving livestock. There have been some statements that the line development procedure might not be as efficient as mass selection, or vice versa. And Wendell Kyle, in his comments yesterday, made the statement that he thought there were many better ways of approaching animal improvement than inbreeding and line crossing.

I think we will challenge Wendell at this point and ask him to elaborate on what he meant by that statement.

DR. KYLE: Well, you have heard some comments here and there about what might be done. In terms of efficiency, I think it should be fairly clear from what has been said that perhaps inbreeding and hybridization in the real sense, going to high levels of inbreeding and testing many lines and hoping to make improvement, would take a tremendous operation, and probably as large or larger than the entire facilities, at least in the large animal work.

So in a positive way, if you accept that -- you may not all do so -- you need to look at what other replacement system or systems might be followed.

First of all, I would say that for the large animals perhaps more attention to mass or individual and family selection for traits that show additive genetic variation of reasonable amounts-- until you take advantage of this, why go beyond this, at least for your primary traits, the traits most important? Why not take care of this, the additive portion which is simplest to take advantage of? I don't think we have done that too well in large animals for the various traits.

After all, there are many traits apparently that are economically important, and I know in sheep work that except for a few traits, I don't think we have yet approached the ultimate limit of using the additive genetic variation, and I am sure this is perhaps even more true in beef cattle, perhaps somewhat in dairy cattle as was mentioned, making good progress with the type of mass and family selection.

These things are the first things to take advantage of and I think a good bit more effort along this line would be worthwhile in livestock species.

How exactly to go about it, what new methods -- I mentioned the possibility of different methods. It seemed to me at the time that the poultry project was revised a few years ago, going from what has been essentially an inbreeding hybridization system to a selection system, comparing various types of selection on the same foundation population, that there was an apparent unwillingness to get very wild in what systems were compared and used. The majority of the people seemed to want to go back to systems that had been used for some time in the poultry, and not try different and varied systems that may or may not work, but at least they should be tried.

Among these -- well, for example, the major one that most people were interested in comparing was family and individual selection for the trait -- in this case it was a single trait -- except for the few that were instituted like the sire-family selection, with and without inbreeding -- these are the only ones, except for the recurrent selection system. There was too much uniformity of what was tried and I think this is true in general in the livestock work.

Among the possibility might be the exploration of -- a little bit of work has been done on selecting on different traits. If you are going to end up crossing strains -- first of all, I think the process in investigating to a large extent advances in selection methods and systems would involve getting away from the point of inbreeding and going to larger groups, selecting the most efficient way various kinds of indexes and traits, if these strains are to be crossed for commercial usage, and then some special things -- I don't think it is clear at all whether or not continuous selection at a high level is the best procedure. Maybe this should be checked in laboratory species first, but both in laboratory species and perhaps slightly in some economic species, when you approach a plateau or continuously highly selected population and show a history of poor reproduction -- it is a most difficult thing. You are trying to maintain these plateaued populations and it is difficult because of reproduction. In fact, in several instances in the lab at Purdue, it has appeared that poor reproduction caused the plateau and stopped you. There seems to be a tendency for some kind of selection -- this is theoretical -- to perhaps cause a genetic correlation between fitness and this selective trait. Pretty soon it stops you and the only way to get around it is to random-mate this population and let it recover.

Well, perhaps some selection procedures could be alternating as far as a high level followed by a lower level or no selection in alternate generations. There are all sorts of ways you can go on various types of selections.

It seems to me a good opportunity exists for -- well, investigating general type environment interaction. Not too much of this has been done in large animals.

Another area I think that is not recognized very well in this country is the sort of thing that Rendel's group in Australia is doing. Their terminology is a little different and so on. But it seems to me that reproduction, particularly in swine and beef cattle, where apparently you have almost zero heritability and have good results as far as improvement from selection, at least by the usual system -- might be to uncover variation or increase phenotypic variation either by applying stress of some type -- this would be the obvious one -- and in laboratory species when you do apply stress for many traits you increase phenotypic variation and sometimes heritability as well. This may make a change in the ability to change reproductive traits.

In Rendel's case apparently selection produced a new variation and the new variation turned out to be additive, which is a surprise to me. And Dr. Goodale is getting to the point of view that selection in the case of a trait not showing much variation at least -- that selection created its own variation. And perhaps this is as good an explanation as any for the selection in the amount of white hair in mice that we have.

In other words, selection hasn't been explored thoroughly. Perhaps a lot of what I am saying about these special things should be tested in the laboratory, but I think some varied methods could be quite useful in large animals that have not been explored. We tend to do too much of the same thing over and over again, I believe.

It is my feeling that fairly large populations kept separate and selected perhaps in different ways, but with the idea of crossing them only to improve reproduction, and that for most other traits you can make a good bit of gain on trying to make use of the additive genetic variation until you reach a plateau. Now here we come to the special situations -- perhaps you are in that in poultry; perhaps not in many of the other species. And then we are going to have to have new techniques here when you come to this, perhaps reciprocal recurrent selection. We are finding in mice that is a pretty weighty method but I am sure by the time you reach that with the large animals there will be techniques in simplifying the procedures involved here.

But I think in some of the large animals, thinking in terms of populations in which you are actually selecting and mating numbers of the order of 15 to 30 males or more -- for example, one of the big poultry producing groups tests 125 males each generation actually in three replicates, so in our large animals in selected populations we aren't doing a very good job in these

terms. You are going to have to have big facilities when you cross-test various strain or breed combinations, after selection -- this is true. And this will require facilities that will handle it.

DR. BAYLEY: Dr. King, I think, asked for the floor.

DR. KING: Well, I don't want to make a speech -- but there are two or three things I want to say. It doesn't seem to me we have really been answering the questions you have up on the board here, getting at the basic issues involved. We have gone into a lot of details about the specific problems but we haven't really answered the question of what our goal should be in livestock improvement, to what is our role in livestock improvement. Are we going to provide the improved livestock for the industry, or are we going to give them the methods? And I think we have to answer that question first before we really decide what kind of research we ought to be doing.

DR. WARWICK: No one replied to Dr. Comstock's analysis of that methodology.

DR. BAYLEY: No one denied his assertion, that if we were to provide the genotypes for improvement, our ability to make a contribution in the inbreeding and line crossing was out of the question. No one denied this. There was no argument.

Is there argument? Does someone believe we should provide the genotypes for livestock improvement?

DR. KING: I think there is a question to be raised. If we say that the livestock industry is not in a position to have large enough facilities to produce the kind of breeding stock they should, and that they are conducting their herd developments and so on with too small numbers to really hope to make any progress, it seems to me they ought to take a fresh look at the laboratory animal work and the experience with poultry and corn where a large number is involved and see where the successes have been.

For example, we have heard very little about what might be done with just the kind of selection that is going on in the meat-proceeding end of the poultry business, where it is straight out and mass selection, with crossing of different breeds. Some of you may not realize that the commercial broiler in most instances is the result of feeding in about six different strains or breeds into the final cross. Usually the male is at least a single cross -- that is the male side of the final cross, and in many cases a 3-way cross, and so is the female. And all of these are produced with primarily just huge numbers of individuals with intense individual selection.

One breeder that I know, breeding a female line -- his whole program is based on raising out large numbers of males in his own operation and selecting off the top 1 per cent. The other 99 per cent he sells as breeding stock to the mass producers in the broiler industry. He saves the 1 per cent to conduct further research on for his breeding operation.

So it seems to me these are some of the things that need to be considered. And it is possible that the livestock industry is not in position to do a breeding job on its own, at least in its present set-up in large animals.

DR. BAYLEY: In this connection I would like to toss a question to Dr. Terrill: Who is going to produce the consumer preferred lamb? Who is going to produce the genotype for it?

DR. TERRILL: We would hope that sheep breeders would, but we will have to show them how. We think we know something about it already.

I would like to direct the discussion a little bit, though, to the questions which Dr. Blackwell asked. I don't think we have gotten directly on those -- maybe we have.

DR. BAYLEY: Let me clarify one thing: You in sheep also do not believe you will be producing improved genotypes by use of the total population?

DR. TERRILL: I sort of feel we cannot answer this. I would think we generally in the past tended to the view that it was our job to produce methods and show how, rather than to do it.

I think we will have to do what is necessary to do to make the livestock industry more efficient and allow it to compete.

DR. BAYLEY: And what are the prospects of sheep breeders accepting the goals of consumer-preferred lamb and producing them?

DR. TERRILL: They may be relatively good; I don't know.

DR. BAYLEY: I merely wanted to make sure we clarified the question that Steve King was raising.

DR. KING: This raises one question, then. If we are not going to produce the genotypes for the industry, are large animals the logical animals to be using the methodology on? Haven't we got better species to work on than large animals?

DR. TERRILL: I think what we will be doing mainly is applying these to large animals and developing methods for sheep breeding. We really still won't be developing the methods themselves or the theory back of it at all. But this gap has to be filled.

DR. KING: If this is the case, why aren't we applying the methods that have proved to be successful, rather than fooling around with one we really have no basic information on as being successful.

DR. TERRILL: I think we are. I think we got stuck with this other thing back when we weren't fully aware of some of these other possibilities. And I think this brings us to the question which I would like to ask: Here we are at this point. We have part of our facilities, not all of them, tied up with these 57 inbred lines. What should we do? Should we just wipe this all out and go to something else? Should we keep some of it? Or should we keep all of it?

I think this is at least one of the questions Dr. Blackwell was asking. We are reaching this decision fairly quickly. I think we have been trying as quickly as we could to get into the position where we thought we could answer this question.

Now I think it is time to ask at least the opinions of these gentlemen, what they think we should do.

DR. BAYLEY: Yes. This is why I pushed the discussion in this direction. If you are considering alternatives, what alternatives would be worth studying?

Do some of you wish to react to that?

Ralph.

DR. COMSTOCK: Let's see -- I am a long ways from the door.

Now, remember, I am just trying this on for size; I am not serious or anything.

I think Steve has raised a real pertinent question, at least a question that needs to be seriously considered. And I say this being faced, I think, with something of the same kind of question in work that goes on at Minnesota.

You say "We have got "57 lines" or "37 lines," or whatever it is, "and they are worth something and we can find out something from them," and it is true; I am sure it is. But at the same time I think we have now, by virtue of the fact that we have come a long

way -- and I think we have come a long way in terms of an understanding since that thing was laid out, and we can think with our eyes wider open about it than we could then. I even heard a little bit of the talk that went on when this was planned. So I think it is incumbent on -- I will say "us" and include me in, even though I am sort of an outhouse man as it were -- to have me say there are some things we can learn from this material, and nobody denies it. Take a look at what alternatively might be learned, using the same money and manpower, with organisms that reproduce faster.

I have become, I must admit, a devotee of small animals. I have a little old mouse laboratory in which, during the years since 1957, we have carried a population of mice for 28 generations. And if I just take a moment for something interesting and it seems to me a little bit pertinent here -- we had a population that was started from a cross of two inbred lines. This wasn't much genetic variation thrown into this pool and we worried about that some. But at the end of 28 generations, as I told you yesterday, there is no doubt but what we have had some effective selection on several characteristics that are of importance, and you can say this is easy because mice weren't selected for that in the past, and this is true and I grant it. Nevertheless, the point I want to make is there has been progress and it has been continuous and it has been linear, and the point I wanted to make was that at the end of 8 generations of that, by gosh I couldn't have stood here and told you we were making progress. Statistically I couldn't have stood here and backed it up. Eight generations in a laboratory with a moderately decent temperature control -- that broke down once in a while -- we had temperature control, a controlled strain, not one of the best in the world, but it wasn't too bad -- and at the end of eight generations we put the statistics on and couldn't say we had moved at all. And, by golly, it scares the life out of me in terms of making decisions about what happens in terms of experiments that run 3 or 5 generations, with not very large numbers and not very good controls, and so on.

DR. WARWICK: How many traits, Ralph?

DR. COMSTOCK: We were selecting for one trait.

DR. WARWICK: Okay.

DR. COMSTOCK: Why do you say okay? What does that prove?

DR. WARWICK: Because I think we feel we have not made a lot of progress in some of our large animal selection, and almost without exception -- well, in no less than 5 and upwards of that, of the traits you are selecting for. And Steve mentioned about the meat strains in poultry. How many were you selecting for?

DR. KING: The primary was growth rate. This is the primary one.

DR. COMSTOCK: I wasn't trying to say because it could be done in mice it could be done in livestock. This is not my point. I don't believe the mice were at the same stage at the outset that the livestock are now. But I believe we can get the mice there and then do some experiments quicker and cheaper than working with livestock.

So all I am saying is that I would think seriously about recommending that a small fragment, 25 per cent of the money you are putting into your beef cattle and dairy cattle and swine, be put over on small animals and I think we can do something with it and you can.

DR. TERRILL: But to come back to this other question, should we be keeping 10 per cent or 20 per cent or none of these lines, or should we keep more?

DR. COMSTOCK: Well, now --

DR. TERRILL: I will agree with you on your first answer.

DR. COMSTOCK: We have to take the point that we are big boys -- no, I put that kind of facetiously but it is true as far as animal breeding you have the cream of the crop right in this room, or at least a big part of it. So we have got to take upon ourselves, it seems to me, the onus of making some judgments that we know may not be correct. In other words, I am telling you that I don't know the answer to your question. I am saying that you know more about sheep and what those lines are worth to you than I do. And if you set out some objectives that you can attain by the use of that material and you know the value of those objectives, then you can answer your own questions.

DR. TERRILL: This will do. I was sort of interested in your opinion along with mine.

DR. COMSTOCK: You see, until you have told me something more than I have heard, I am saying they are worth something and you can find out something, but I suspect with the same money and

manpower we can find out more somewhere else.

DR. KYLE: I would just throw out a suggestion that may not be correct: Obviously, certainly beyond 1970 -- if you want to go on through the test to find out what you do have, but I would say no more than 4 lines of Rambouillets and 4 of Targhees and 2 of Columbias. This would be the upper limit.

DR. BAYLEY: Why?

DR. KYLE: For the reason I don't think -- you mean whether you should save any or not?

DR. BAYLEY: No.

DR. KYLE: If you want to do anything with them, one is to maintain material where perhaps in each case it is the line that has the highest inbreeding. You are talking about testing physiological differences. At least have a few lines available for this. The more highly homozygous the better, at least estimated homozygosity -- perhaps on the basis of merits, if you wish that. I find that desires for what you want to do change over time and you always have to keep in the back pocket a little of this material that may be useful later. If you throw it out, here is 30 years of work down the drain. But I would say four lines because this would be enough for a 4-way cross in the two sets and the Columbias are so much alike I think two would be enough there.

DR. KINCAID: I would like to put in a word here and maybe you will think I have changed horses.

But Chuck Shelby referred to this hundred-and-some lines which were started in the swine lab, inbred lines, and about all we know about them is how fast they grew and how many pigs they had. We know nothing about what we did to the biochemistry and physiology of these pigs.

It seems to me that where we have genetic variability, either from selection experiments, or from the development of inbred lines, that here is a golden opportunity to begin to look under the skin and see what we have done to these animals and begin to understand a little bit about what genetic changes do to the physiology and biochemistry of these animals.

Now, in human medicine they have put the finger on something like 300 so-called errors of metabolism. Some of them can be identified by very simple tests. Some of them have been associated with abnormality in the gross chromosonal picture.

Here again we don't even know for sure what the number of pairs of chromosomes are in these large animals. And there is

extensive crossing, both in pigs and in sheep, and isn't it quite possible that there may be floating around at least some partial similarity to what you get in the mule when you cross the horse and the ass, where none of the chromosomes pair?

So that starting from a cross, and then following this cross up, there is the possibility that you could run into trisomics in the absence of pairs of chromosomes and other gross things of this sort that might have quite an important bearing on what we might be able to do from the quantitative standpoint.

Perhaps maybe we should tie into the opportunities that we have to try to get out as many of these simpler genetic things that may be floating around that have big influences, and in this way be able to get a little more precise information on what the situation is from a quantitative standpoint.

I am thinking that perhaps we might put a little more emphasis into physiology and biochemistry even if we had to do it at the expense of biometry.

DR. COCKERHAM: I want to speak to the question before that. Does anyone want to speak to this comment?

DR. BAYLEY: Does anyone want to comment on these alternative uses of these inbred lines, particularly in this case because of their feasibility for supplying stock for physiological studies?

DR. WARWICK: Perhaps a pertinent comment might be that we already have breeds in existence that we know nothing about in maybe equally or perhaps even more intersting sources of material.

DR. BAYLEY: In other words, there perhaps are easier ways getting the variability you need.

DR. COCKERHAM: I want to comment on this idea of saving 4 lines when you don't have facilities to do anything with them, so to speak. It seems to me you have to either decide to go on with making your lines and crosses among strains or breeds or whatever you have, or to get rid of them. I don't see four. All that is going to do is dilute anything you do.

DR. TERRILL: You are saying all or none?

DR. COCKERHAM: That is right. If you can't do one, you certainly can't do two things, you see, or three things or four things, or so forth.

I think that is part of the problem already, that the facilities in any one place are probably not such that any one thing can be done well.

If you go back to family or mass selection like this, I think it is very important to have a fairly good-sized population, and you want to select fairly heavily -- probably the most important feature concerned in whether you get into difficulties, fertility and things like this, has to do with the number of parents that you save more then the proportion that you save, you see. One might guess that in part.

So in terms of long-term -- well, there are two kinds. There is the theoretical or Monte Carlo evidence -- I am not sure it is experimental evidence. Your most efficient -- not most efficient, but from the standpoint of the long-term gain it is better to select, for example, to 50 per cent intensity. Well, maybe it is kind of a flat-topped curve on this, so maybe 30 per cent. But I certainly don't think one should go whole-hog in selecting 1 per cent and so forth until he can truly save a lot of individuals.

Well, did you have facilities? I am not too much acquainted with your facilities available here for any of these various types of programs.

The dairy people are using the cattle of the country, actually -- maybe not in the most efficient manner, but they have got really a large population size, and I think they have been quite effective. You might work up something with evaluation techniques and AI in beef cattle. If you start weighing some of these animals on a large scale, it might be astounding the progress you could make.

DR. TERRILL: Are you saying you don't think these tests we are making now are going to be useful in telling us which lines will be useful in the future?

DR. COCKERHAM: No, I don't.

DR. TERRILL: Maybe we are wasting our time making the tests now.

DR. COCKERHAM: Yes. I think you should either go on with the job -- possibly eliminate some of the poorest ones, if you have facilities to do it. But you get in trouble with these facilities to test. Ideally I think early testing of your lines is better -- I say "ideally" -- but this requires --

DR. TERRILL: We see our way clear to complete the tests we have in mind. It is not easy but I think we can get it done.

DR. COCKERHAM: Do you disagree with that? I would like to have your comments.

DR. COMSTOCK: I am kind of in a haze because I am not quite sure what the objectives are.

DR. COCKERHAM: Animal production.

DR. BAYLEY: I would like to mention that, too, Clair. I think you are confusing us a little. You say you do not believe you should produce the genotypes but suggest the possibility of testing these lines to know what lines you should continue.

DR. TERRILL: Our idea was perhaps we could accomplish as much with these lines but cutting them in half or going as far as Wendell says and leaving us room for facilities for other things we should be doing. I agree with a lot that has been said.

DR. BAYLEY: But my point is: Are you trying to test a method or find an improved genotype?

DR. TERRILL: We are trying to do both.

DR. BAYLEY: I suspect that is true.

DR. TERRILL: But do we have to keep all these lines for an indefinite period to test the method?

DR. BAYLEY: I wanted to make sure your goals are clarified, because once you deny the production of a genotype --

DR. TERRILL: I don't think I would agree to deny it, either.

DR. COCKERHAM: You don't have enough lines to test it in the first place.

DR. TERRILL: So maybe the only thing we can hope to gain is contribute something to the improvement of sheep through the actual animals we produce.

DR. KYLE: My point in the numbers was deciding that after you are done testing you are through with the inbred hybridization system -- it was maintaining this material. So such things as Dr. Kincaid was talking about, the need at some future date or at the immediate time to look at differences between them -- I would certainly pick them on the basis of wide differences. We have found in the mouse lab where we want to test some biochemical factor in mice, we send to Bar Harbor and get a couple of inbred lines, preferably quite different, hopefully on the trait we are going to measure, and measure on the inbred lines supposedly completely homozygous, and the crosses between them, and go on from there to a non-inbred population. This simplifies your techniques a little bit.

That is a starting point on some of these techniques.

DR. KING: I would just like to remind you of what Dr. Sprague said earlier, that only one in a hundred lines tends to be good enough for you to double-cross and then on the basis of a survey they find only one in ten of those released actually survived in commercial production. And I think we could say that of the inbred lines that the public institutions released to the poultry industry, our record has certainly been no better than that, if as good.

I know some years ago on two different occasions I have been through this same sort of involvement with what to do with inbred lines we had in poultry. To the best of my knowledge, the last releases we made from Beltsville -- none of those have survived.

DR. COMSTOCK: This is a good opportunity for me to get on both sides of the fense. When we revised the swine project at Minnesota we raised the question of what to do with the old "M" line, which was 95 per cent inbred, so we decided to get rid of it and they took it down to Ames and have been quite happy that they did because they did some blood group work and so on.

DR. BAYLEY: Certainly this is a sensible approach, if you have developed something that might be of use to others, let them have an opportunity to use them.

I am going to bring this discussion to a close. I think we have had a tremendous exchange of ideas. It has been going on without any prodding since a little after two o'clock and the time is now nearly 4:45.

You have been a very fine group to moderate. The openness and willingness to get deeply into these problems has been marvelous. I want to compliment our panel on their willingness to delve into our kinds of problems and the freedom with which they have exchanged ideals.

Perhaps I am being quixotic to make any concluding remarks, and yet I think there are a few that should be made.

One of the most significant things that has been said in this discussion is the fact that today, because of our training and our past experience and our past mistakes in planning and developing and directing our livestock research, we now have considerable know-how in appraising the directions we should go, in deciding among the alternative projects, which ones we should undertake.

But I think I am also safe in saying that we really haven't started to use this know-how to the fullest extent possible. We

sometimes are vague in our goals. We sometimes give the impression to other people, as well as to our own colleagues, that we are carrying on this research because we have the animals and we want to make use of them.

I want to assure you that animals are expendible today in the minds of those who are allocating research funds. Those who are trying to support our research have no feeling that because we have the animals we should therefore have the money to do something with them. They are interested in what kind of problems we are trying to solve and what the requirements of those problems are. The animals are nothing but a means to the end and they can be eliminated if it means a better allocation of our resources for other purposes.

I think we need to keep this concept clear in our planning and in our thinking.

These considerations force on us the question which you raised yourselves: When we are considering research involving making plans with livestock, we have an obligation to decide whether there has been adequate work with other organisms to justify the expense with large animals. The answer to this question should be a part of our justifications in proposing either the continuation of current work or the initiation of new work.

Furthermore, when we are approaching alternative projects, we have the obligation today, as was so often pointed out by our panel members: Either do the job right or don't start it. And I can't emphasize this too much. Because we should tackle those things which we can accomplish. When we get into research which can only partially answer the questions raised, we weaken our program all the way down the line.

You see, I have committed myself. I didn't expect that my concluding remarks would come out quite this way, but I think these thoughts are something we should take home with us. Each of us should evaluate our individual projects in this respect when we are thinking of what we are doing now as well as what we are going to do in the future.

I don't want to scare anybody, and yet at the same time I would neglect my own understanding of the problem and my duty to you if I did not say that the next several years ahead are critical years regarding the extent to which we can go ahead and advance in our livestock research. We have to make our research program just as solid as possible, and we have to be willing to produce justifications which will hold up against all kinds of criticism.

With that, it has been a wonderful meeting and I thank you very much for the opportunity to participate in it with you.

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